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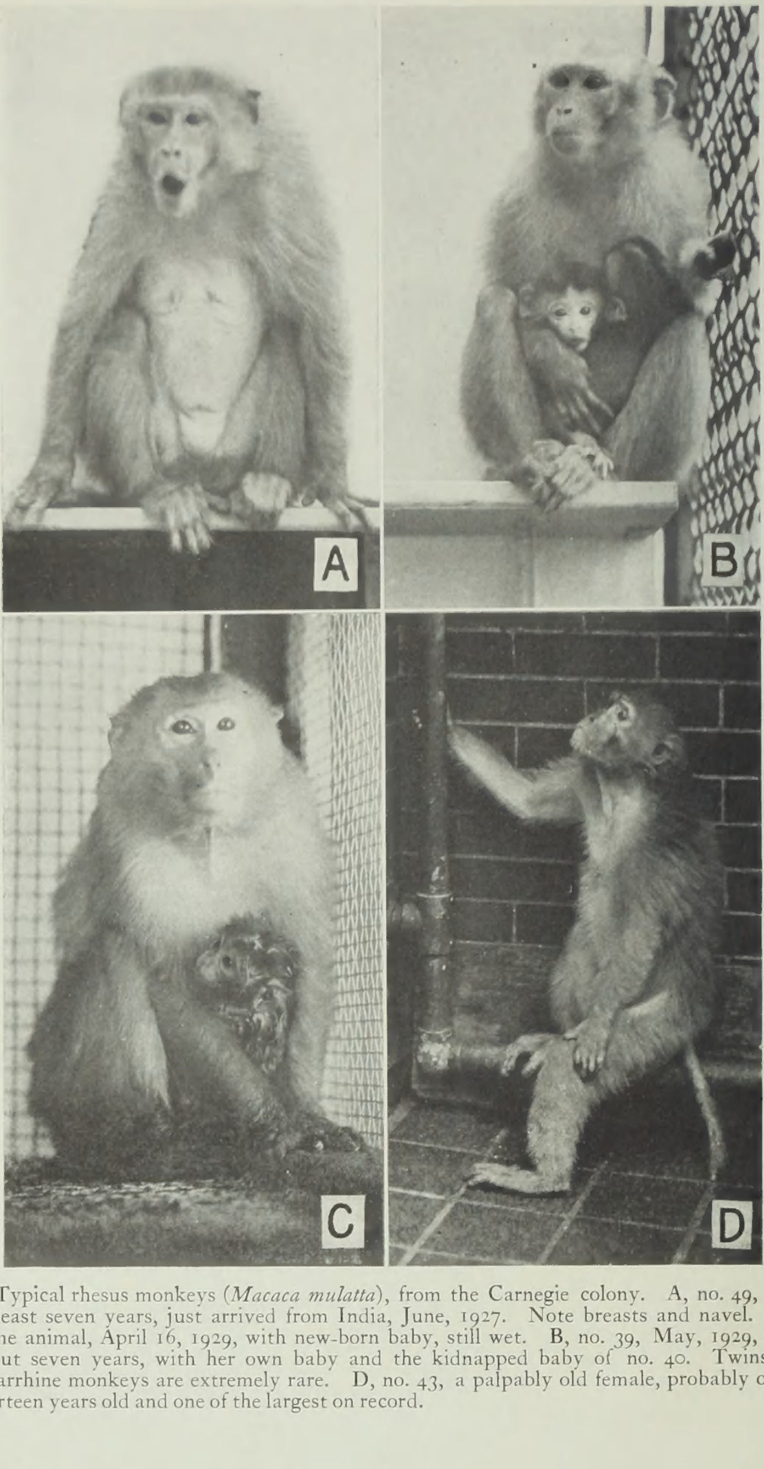
THE ANATOMY
of
THE RHESUS MONKEY



Typical rhesus monkeys (*Macaca mulatta*), from the Carnegie colony. A, no. 49, age at least seven years, just arrived from India, June, 1927. Note breasts and navel. C, Same animal, April 16, 1929, with new-born baby, still wet. B, no. 39, May, 1929, age about seven years, with her own baby and the kidnapped baby of no. 40. Twins in catarrhine monkeys are extremely rare. D, no. 43, a palpably old female, probably over fourteen years old and one of the largest on record.

THE ANATOMY
of
THE RHESUS MONKEY
(*Macaca mulatta*)

by

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BALTIMORE
THE WILLIAMS & WILKINS COMPANY
1933

Copyright, 1933
THE WILLIAMS & WILKINS COMPANY

Made in the United States of America

Published November, 1933

Composed and Printed at the
WAVERLY PRESS, INC.
for
The Williams & Wilkins Company
Baltimore, Md., U. S. A.

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PREFACE

The need for a handbook on the anatomy of the rhesus monkey has become more and more evident in recent years with the greatly increasing use of this species as a laboratory animal. The project assumed concrete form when Dr. W. E. Sullivan of the University of Wisconsin called a conference of interested persons at the Charlottesville meeting of the American Association of Anatomists in 1930. The editors were asked to organize a staff of contributors, to which task they acceeded upon the assurance of hearty cooperation, which promise has become a reality.

The present work was not designed as a textbook in the ordinary sense, but rather as a handbook, presenting as it does, in eighteen chapters, the independent researches of eighteen individuals. The book is to be judged as a pioneer, since it represents the first comprehensive anatomy of an old world monkey. A certain lack of that balance that should characterize a textbook was inevitable. Any attempt to imitate for the monkey the textbooks of human anatomy, which have become standardized after hundreds of years of research, would have been futile. It seemed best to outline the general purposes of the book and to leave the manner and comprehensiveness of execution to the judgment of the individual authors and to the time at their disposal. It is believed, however, that the book attains the immediate object of affording a useful description of the anatomy of the rhesus monkey for research workers as well as for such classes in comparative anatomy as contemplate using this animal as the object of dissection. Certain chapters might be considered unduly long if the textbook yardstick were strictly applied. Yet the results of the authors' researches are published in full and will doubtless be useful to a great variety of workers.

Another disparity between the present study and human anatomies is found in the limited number of monkey specimens that could be dissected. From thousands of human bodies that have been dissected and described, the range of variation in many of the organs is rather well known. Not so with the monkey. Persons using this book in connection with further dissections will encounter specimens varying in one particular or another from those on which the descriptions in this book are based. Some slight discrepancies even exist among the different chapters of this book, due

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to variations in the specimens studied by the various contributors. Only a few published studies on ranges of variation in the rhesus monkey exist and some of these are quoted in the appropriate places in the text. The editors will welcome information concerning further deviations encountered by other workers and will undertake to record the variations found, so that they may be included in any new edition that might be demanded.

The various chapters differ in content as well as in length. It is apparent that some data can be set down more or less categorically and definitely and will need little revision. The chapter on growth and development (II), on the other hand, would be especially subject to revision as more specimens are studied. Though not complete, however, these data should prove exceedingly helpful to experimenters in many fields, for up to the present time there have existed no reliable data for estimating even approximately the age of monkeys. With the aid of the tables in chapter II this desideratum is now attained for the rhesus monkey.

Aside from weight and size, certain other bodily characteristics are useful in estimating the age of a given monkey, namely, ossification of the bones and calcification and eruption of the teeth. Unfortunately it was not possible to publish here more than a few roentgenograms (see figures 17 and 21). The many others that were made will be reserved for subsequent studies.

The eruption of the teeth is presented in two sets of data (chapters II and VI). There would at first glance seem to be a great discrepancy in the figures; but when the criteria for eruption as defined by the two contributors is considered, their data are seen to supplement one another, as has been set forth in footnote 1 in chapter II.

Allusions to the comparative anatomy of primates abound throughout the text, especially in chapter VII. These data are in large part gleaned from the literature, in small part from personal observation. Nevertheless, the contributors should not be held responsible for omissions in this regard, inasmuch as it was manifestly impossible, within the limits of the volume, to discuss the entire literature on the anatomy of primates. Each chapter of the present work represents mainly a description of structures as found by the authors in the specimens used.

The Basle anatomical nomenclature (B. N. A.) is used. It seemed best, for various reasons, to employ the terminology of human anatomy rather than that of comparative anatomy.

The bibliographies to the several chapters include only the more important references, more particularly those which themselves contain good bibliographies. From these the student may procure more exhaustive lists for further readings on the anatomy and biometry of primates. They are in no wise to be regarded, however, as lists of publications referred to in the text. Especial attention is here called to the following general works:

Martin, Rudolph. 1928. Lehrbuch der Anthropologie. vol. III, 2nd ed., Jena.

Keith, Arthur. 1896. An introduction to the study of anthropoid apes. Natural Science, London, vol. 9, pp. 26, 250, 316, 372.

Sonntag, Charles F. 1924. The morphology and evolution of the apes and man. London.

Weber, Max. 1927/28. Die Säugetiere. 2nd ed., 2 vols., Jena.

The editors were fortunate in securing as artist the services of Mr. Benjamin Kopel, who executed all of the drawings except the very few especially accredited to others.

Carl G. Hartman,
William L. Straus, Jr.

Baltimore, July 21, 1933

CHAPTER I

THE GROUPS AND NAMES OF MACAQUES

GERRIT S. MILLER, JR.

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INTRODUCTION

The macaques are the monkeys most frequently used as laboratory animals, a distinction that they owe to their convenient size, their hardy constitution, and their rather omnivorous natural diet. This combination of peculiarities makes them easy to transport and not unduly hard to keep captive in good health. In particular, the best known of them all, the rhesus macaque, may owe some of its special fitness for laboratory purposes to physical characteristics that have enabled this species, in nature, to attain a wider geographical and altitudinal distribution than any other Asiatic monkey. According to the latest authority, Pocock (Jour. Bombay Nat. Hist. Soc., vol. 35, pp. 530–551, February 15, 1932), the range of the rhesus extends across nearly the entire northern half of the Indian peninsula, then north through the Himalayas up to 5,000 or 6,000 feet in Kafiristan, Chitral and Kashmir. Eastward the range continues across Burma, Siam and French Indo-China to the region of Hong Kong and Fokien in South China, and into the Provinces at Szechuen in West China and Tche-li in North China. In this great area six different geographical races are now recognized. The one most commonly found in captivity is the North Indian race.

THE MACAQUES

The word macaque is the French form of the Portuguese "macaquo" derived from the Congo name of some African monkey of an entirely different sort. About one hundred and seventy years ago the French naturalist Buffon made the mistake of supposing that a Malayan "crab-eater" was a "macaquo" from the Congo. The usage that he then wrongly established (Histoire Naturelle, vol. 14, p. 190, 1766) has now become permanently fixed.

As a genus the macaques have been technically characterized by Forbes (A hand-book to the primates, London, Edward Lloyd, Ltd., vol. 2, pp. 1–3, 1897) as follows:

> "This genus embraces a large number of species which are characterised by having a thick-set body and short stout limbs, with the thumb set backward. The muzzle is con-

siderably produced and rounded, but the nose does not extend as far out as the plane of the upper lip; the nostrils open in advance of its termination, and are directed obliquely outwards and downwards; their cheek-pouches are large, and their lips thick and protrusile; their eyes are approximated, and look out from below thick and prominent superciliary ridges; their ears are naked and applied flatly to the sides of the head and their hind upper angle is pointed; their callosities, which extend with age, are often surrounded by a portion of the buttocks, which is always nude. The tail is long, short, tufted, or reduced to a mere tubercle, and it may be quite invisible externally. Some have the hair of the head long, and radiating in all directions; others have the face encircled by a kind of mane. In some northern forms, the whole body is covered with a woolly fur, as a protection against cold."

"In the skull the facial region predominates over the cranial, and the lower margin of the frontal bones are exserted to form a thick prominent ridge over the orbits and nose; the mastoid process on each side of the skull, behind the ear, is very prominent for the attachment of a muscle which assists in opening the mouth and in swallowing their food. Strong muscles also stretch from the back of the head to the spine for the support of the head. The canine teeth are long, and press against the anterior pre-molars of the lower jaw, the position of which is modified or distorted by the pressure, thus enabling these animals to crush and open hard-shelled fruits. Their anterior and median lower molars are four-cusped, while the posterior is markedly larger, and has five cusps and a posterior talon. The carpus, or wrist, possesses the central (*os centrale*) bone, and the fingers have their metacarpal bones elongated. The caudal vertebrae in the species of this genus are usually numerous; even in the short-tailed species they vary from fifteen to seventeen in number, the reduction in the length of the tail being the result of a great diminution in the size, not in the number, of the vertebrae. In the tail of one species (*M. sylvanus*), however, they are reduced in number to two or three; in the same species the tail lacks the

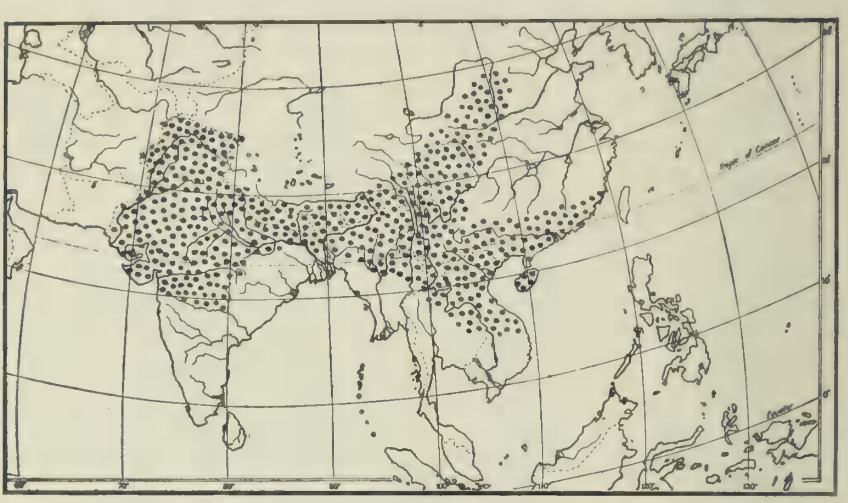

FIG. 1. Approximate distribution of the races of the rhesus monkey.

chevron (or V-shaped) bones on its under side as well as the processes to which the muscles for its movement are attached. Most of the Macaques have a throat-sac, which communicates with the larynx under the thyroid cartilage, and which fills with air, acting as a resonator to their voice."

"The Macaques are among the commonest Monkeys of India and the East Indian islands. They occur also in Northern Africa (Morocco), and in Gibraltar, across the Straits. Eastwards they extend into Thibet, Northern China, [Japan and the Philippine Islands.] They are also found in Sumatra, Java, Borneo, Celebes, Timor, [and on many of the small islands of the Malay Archipelago.]"

Many different kinds of macaques are known, exactly how many it is impossible at present to say. In 1912, Elliot enumerated 53. Others, unknown to Elliot, have been discovered during the past two decades. But whatever their exact number may eventually prove to be, the species appear to fall rather naturally into ten main groups that are distinguishable from each other by physical characteristics appreciable in living captive animals. In the key on page 5 the present author has attempted to set forth these characteristics in non-technical language. The names of the groups that contain the kinds most likely to be found alive in laboratories are printed in bold faced type.

NAMES

The technical names of the macaques have been the source of a great deal of annoying confusion, most of which has resulted from the failure of zoologists to follow uniformly the simple rule that the right name for an animal is the name first given to it.

(*1*) *Generic names*

As a clearly recognizable special genus of monkeys, distinct from the earlier, all-inclusive "*Simia*," the macaques were first designated under the name *Macaca*. This was done by the French zoologist Lacépède in 1799 (Tableau des div., sous-div., orders et genres des Mamm., p. 4). Another Frenchman, Desmarest, arbitrarily altered Lacépède's name *Macaca* to *Macacus* in 1820 (Mammalogie, p. 63). Apparently for no better reason than that Desmarest's work was more widely known than Lacépède's the incorrect *Macacus* came into general use. Not until 1904 was the error definitely pointed out (Palmer, Index Gen. Mamm., p. 390); and even now *Macacus* often appears in print.

In 1909, Elliot (Ann. and Mag. Nat. Hist., ser. 8, vol. 4, p. 250, September, 1909) discovered that the name *Pithecus* had been proposed in 1795 (E. Geoffroy, Mag. Encyclop., vol. 3, p. 462) for an assemblage of species that were, for the most part, macaques. He therefore substituted *Pithecus* for *Macaca*, and so used it in the second volume of his Review of the Primates, 1912 (pp. 176–253). Four years later, however, Thomas showed that there were other animals as well as macaques among the species originally placed in the genus *Pithecus*, and that, according to the International Code of Zoological Nomenclature, the name should be applied, not to the macaques as Elliot had done, but to the very different monkeys known as langurs (Ann. and Mag. Nat. Hist., ser. 8, vol. 17, pp. 179–181, February, 1916). The history of *Pithecus* is further complicated by the fact that this name was applied by Cuvier in 1800 (Lecons Anat. Comp., Tabl. 1) to the two anthropoid apes then known, namely the orang and the chimpanzee, and that it has subsequently been often used for the orang. Therefore, after giving all these facts long and minute consideration, the International Commission on Zoological Nomenclature has ruled that *Pithecus* shall be suppressed on the ground that its retention as a technical name for any primate "will produce greater confusion than uniformity" (Opinion 114. Smithsonian Misc. Coll., vol. 73, no. 6, pp. 25–26, June 8, 1929).

This decision leaves *Macaca* as the officially approved designation of the macaques, so long as all the species are regarded as members of one genus. If several genera of macaques are to be recognized, as seems to be the not improbable result to be expected of a more careful study than has yet been made, the name *Macaca* would have to be restricted to the Barbary ape, because that animal was the only one that Lacépède mentioned by name when he established the genus. For the present, however, all the common "laboratory" macaques can be safely called *Macaca*, with the understanding that, if an exact designation is desired to indicate each of the special groups now regarded as subgenera, the names for those groups to which the laboratory animals belong are as follows:

For the rhesus macaques, *Maimon* Wagner, 1839 (Schreber's Säugethiere, Suppl., vol. 1, p. 141);

For the crab-eating macaques, *Cynamolgus* Reichenbach, 1862 (Vollständ. Naturgesch. Affen, p. 130);

For the bonnet macaques, *Zati* Reichenbach, 1862 (Vollständ. Naturgesch. Affen, p. 130).

Another generic name whose occasional use for the macaques needs explanation is *Silenus* Goldfuss, 1820 (Handbuch Zool., vol. 2, p. 479). This name was based on the very peculiar lion-tailed monkey, or wanderoo, of the Malabar Coast region, India. If it be agreed, as Elliot assumed in 1912, that the Barbary ape is generically distinct from the macaque group, and that the wanderoo belongs in the same genus with the ordinary macaques, then, and then only, does *Silenus* become the correct generic name for the macaques as thus understood. This was explained by J. A. Allen in 1916 (Bull. Amer. Mus. Nat. Hist., vol. 35, pp. 49–52). But so much doubt has been felt with regard to both of these assumptions that *Silenus* has not been widely used. Stiles and Nolan, however, adopted this name in their Key-catalogue of primates for which parasites are reported (U. S. Treasury Dept., Hygienic Labor-

KEY TO THE MAIN GROUPS OF MACAQUES

- Tail at least as long as backward-extended leg and foot (usually much longer)
  - Hairs on sides of head and neck conspicuously elongated, lax, their color grayish in striking contrast with clear blackish body and limbs; tail about as long as backward-extended leg and foot .... *silenus*-group
  - Hairs on sides of head and neck not elongated and not conspicuously contrasted with slightly grizzled brownish, yellowish or grayish body and limbs; tail much longer than backward-extended leg and foot
    - Hairs on top of head conspicuously elongated, these long hairs always radiating from a common center in such a manner as to form a "cap," "bonnet" or "toque," an obvious trace of which is present in very young individuals **radiatus**-group
    - Hairs on top of head not conspicuously elongated, these normally long hairs occasionally radiating from a common center but never in such a manner as to form a "cap," "bonnet" or "toque" .... **irus**-group
- Tail obviously shorter than backward-extended leg and foot, in some species scarcely or not visible in the living animal.
  - Length of tail greater than length of hind foot from heel to tip of longest toe
    - Hairs on tail spreading (about like those of a house cat in adults); hairs on top of head directed uniformly backward; hairs below and in front of ears directed backward .... **mulatta**-group
    - Hairs on tail closely appressed to skin; hairs on top of head short and stiff, radiating sideways and backward from a median crown spot that is usually extended toward forehead as a narrow "part;" hairs below and in front of ears directed forward .... *nemestrinus*-group
  - Length of tail less than length of hind foot from heel to tip of longest toe (tail sometimes reduced to a mere scarcely visible rudiment).
    - Tail always evident and always covered with a dense growth of long hair essentially like that on neighboring part of back .... *fuscata*-group
    - Tail sometimes not evident, its hairy covering, if present, short, sparse and unlike that of neighboring part of back.
      - Hair on median region of forehead shortened and close-lying in noticeable contrast with the elongated, lax hair of back and sides of head and of back and sides of body .... *arctoides*-group
      - Hair on median region of forehead normal (not shortened and close-lying in noticeable contrast with that of the region behind it)
        - Color of back, when fur is disarranged, conspicuously variegated, by contrast between the dark slaty bases and light tips of the hairs .... *sylvanus*-group
        - Color of back, when fur is disarranged, not variegated by contrast between color of bases and tips of the hairs (Celebean macaques)
          - Head with a median longitudinal crest of elongated hairs; an almost hairless area on each side of forehead in front of ear .... *niger*-group
          - Head with no unusual arrangement of hair (that of occiput or of forehead sometimes elongated) .... *maurus*-group

atory Bull. No. 152, pp. 528-537, 1929), a pamphlet that is well known to laboratory workers.

(2) *Specific names*

On turning to the specific names we find no less confusion.

(*a*) *The rhesus macaque.* During the second half of the eighteenth century the rhesus macaque was well described by two naturalists who had not adopted the then recently proposed but now universally followed binomial system of Latin names for animals. Pennant, in England, saw a rhesus that had been brought alive from India. In his Synopsis of Quadrupeds, 1771, he entered this animal as the "Tawny Monkey" (p. 120). Buffon, in France, had an equally clear idea of the rhesus, though he did not know exactly where his specimen came from. Because of its short tail as compared with that of the crab-eating macaque he called the animal the "Macaque à queue courte" (Histoire Naturelle, Suppl., vol. 8, p. 56, pl. 13, 1789).

By the end of the century each of these descriptions of the rhesus had been made the basis of two technical specific names by writers who were consistently following the system that we now use. Pennant's "tawny monkey" received the specific names *mulatta* in 1780 (Zimmermann, Georg. Gesch. des Menschen, vol. 2, p. 195) and *fulvus* in 1792 (Kerr, Animal Kingdom, p. 73); Buffon's "macaque à queue courte" was technically designated as *rhesus* in 1799 (Audebert, Hist. Nat. des Singes., fam. 2, p. 5, pl. 1) and as *erythraea* in 1800 (Shaw, Gen. Zool., vol. 1, p. 33). Through a general failure to recognize the rule that the first name is the right name, the third of these designations in point of date, namely *rhesus*, gradually became current. So it remained until 1921, when the long-standing mistake was explained by Hinton and Wroughton (Journ. Bombay Nat. Hist. Soc., vol. 27, pp. 665-668). As English words "rhesus" and "rhesus macaque" are unobjectionable; but as a technical name *rhesus* is incorrect. In the language of science the most common laboratory monkey must be known as *Macaca mulatta* (Zimmermann).

(*b*) *The crab-eating macaques.* In the tenth edition of his Systema Naturae, 1758, the work that forms the starting point of the binomial system of naming animals, Linnaeus included on page 28, a "*Simia cynamolgos*" (altered to *cynomolgus* in the twelfth edition, 1766, p. 38) from Upper Egypt. This animal was the hamadryas baboon, which he had already described as *Simia hamadryas* on the preceding page. Sixteen years later Schreber (Säugethiere, vol. 1, p. 91, pl. 13, 1774) formally transferred the Linnaean name to an entirely different animal, the "Macaque" of Buffon (Histoire Naturelle, vol. 14, p. 190, pl. 20, 1766) which he, like its original describer, supposed to be an African species identical with the *Simia cynamolgos* of Linnaeus. There can be no doubt, however, that Buffon's macaque was a Malayan "crab-eater" of some kind, an animal bearing no close resemblance to a hamadryas baboon or to any African monkey. In this incorrect sense the name "*cynomolgus*" passed current for more than 100 years.

During the nineteenth century the mistake was recognized by some writers, for instance, by F. Cuvier in 1818 (Mém. Mus. Nat. Paris, vol. 4, p. 120) and by Blanford in 1888 (Fauna of British India, Mammalia, p. 23); but the consensus of opinion was to the effect that "the name [*cynomolgus*] has been used too long [for the crab-eating macaque] to be altered now with a probability of a less familiar term being generally accepted" (Blanford).

The first serious attempt at reform was made by Bonhote in 1903 (Fasciculae Malayenses, Zool., vol. 1, p. 3). He definitely proposed to discard the name *cynomolgus* for any macaque and to use in its stead the *fascicularis* of Raffles (Trans. Linn. Soc. London, vol. 13, p. 246, 1822) based on the crab-eating macaque of Sumatra. Seven years later Cabrera showed (Ann. and Mag. Nat. Hist., ser. 8, vol. 6, p. 620, December, 1910) that *fascicularis* is antedated by *irus* F. Cuvier, 1818 (Mém. Mus. Hist. Nat. Paris, vol. 4, p. 120), a name applied to the same Sumatran animal.

Contrary to Blanford's prediction these corrections were welcomed by systematic workers. It is true that Elliot, in the second volume of his Review of the Primates (1912), either because he overlooked Cabrera's findings with regard to the original locality of F. Cuvier's *irus* or because he doubted them, used the name *irus* for the crab-eating macaque of the Malay Peninsula (p. 229), an animal that apparently differs slightly from the one found on Sumatra (for which he retained the designation *fascicularis*, p. 233). But the term "*cynomolgus*," which Blanford believed to be permanently established in spite of all rules, has now disappeared from the nomenclature of the macaques.

While any macaque of the *irus*-group is at once recognizable by the long tail and the lack of strikingly peculiar hair growths on the head and neck, the determination of the exact local species represented by a living animal whose history is not known is a matter of difficulty. There may be as many as two dozen of these local species scattered on the Malay mainland and islands all the way from the Nicobars to the Philippines.

Individuals captured at almost any point in this wide area are likely to appear in the live animal trade as "crab-eating macaques." Although not always obvious in single individuals, particularly when immature or in bad condition, the vârious distinctive characteristics of these local species are, for the most part, so well defined that they may be accompanied by differing physiological peculiarities. Laboratory results obtained from the study of the Nicobarean *Macaca umbrosa*, for instance, might therefore differ from those based on the Sumatran *M. irus*, or on the Javan *M. mordax*, or on the Philippine *M. syrichta*. Great care should always be taken in tracing the history of any *irus* macaque used for experimentation.

(*c*) *The bonnet macaques.* There are two kinds of bonnet macaques, either one of which is likely to be found in an animal dealer's stock, namely, the browner, duller-colored, true "bonnet" of Madras, and the redder, brigher-colored "toque" of Ceylon.

In 1766, Buffon described one of these animals (Histoire Naturelle, vol. 14, pp. 241–243, pls. 30–31). He called it the "Bonnet-Chinois" because the long, radiating hairs of its crown formed a cap or bonnet that resembled, he said, the head-dress in use among the Chinese. A few years later Linnaeus gave Buffon's animal the technical name "*Simia Sinica*," the Latin equivalent of "Chinaman monkey" (Mantissa Plantarum, p. 521, 1771). Buffon thought that his "bonnet-chinois" came from Bengal. But in this supposition he was wrong, as is proved by two subsequent descriptions (each accompanied by a colored plate) based on his original specimen, and published, respectively, by Schreber in 1774 (Säugethiere, vol. 1, p. 109, pl. 23), and Audebert in 1799 (Hist. Nat. des Singes, fam. 4, p. 18, pl. 11). These show that the animal was a bright colored Ceylonese "toque." Nevertheless the name *sinica* has been commonly applied to the brown Madras "bonnet." This mistake was explained by Hinton and Wroughton in 1921 (Journ. Bombay Nat. Hist. Soc., vol. 27, pp. 813–815), and the distinguishing characteristics of the "toque" and "bonnet" were elaborately set forth by Pocock in 1931 (Journ. Bombay Nat. Hist. Soc., vol. 35, pp. 276–288).

It has thus been made clear that the Ceylonese "toque" and not the Madras "bonnet" must be known as *Macaca sinica*.

For the "bonnet" of southern India the correct name is *Macaca radiata*. The name *radiata* dates from 1812, when Geoffroy applied it to a monkey probably obtained from a menagerie (Ann. Mus. Hist. Nat. Paris, vol. 19, p. 98), and therefore without any definite history. His account, however, supplemented by the figure and description published in 1820 by F. Cuvier (Hist. Nat. des Mamm., vol. 1, livr. 18, pp. 1–2) shows that the animal was a Madras macaque.

During the period when the "bonnet" or Madras macaque was wrongly known as "*sinicus*" the Ceylonese "toque" was usually called "*pileatus*." But the name *pileatus* cannot be used for this macaque or for any other. It originated with Kerr, who, in 1792 (Anim. Kingdom, p. 69), applied it to the "bonneted monkey" of Pennant's History of Quadrupeds, a monkey that it is now impossible to identify. That Pennant's "bonneted monkey" was neither of the animals in which we are here interested is evident, because it had black arms and legs and because its crown was surmounted by a "circular bonnet" composed of "upright black hairs."

CHAPTER II

GROWTH AND DEVELOPMENT

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There exists as yet very little information in regard to the growth changes in monkeys of actually known age. The published records for the macaque consist merely of a few notes by Lashley and Watson (1913) on the age of eruption of some of the deciduous teeth in a rhesus macaque and of the brief account by Spiegel (1929) of the growth during the first six months of two Java macaques. Our knowledge of the prenatal growth of the macaque is restricted to the brief description of two fetuses by Toldt (1903) and to a few data published by the writer (1926).

During the last few years the author has had the opportunity of following the growth of more than twenty of the animals born in the Carnegie Colony of rhesus macaques. Chiefly through this study it has become possible to outline at least in a preliminary way some of the changes with advancing age in one of the many species of macaques. It must be emphasized that the tentative averages, as listed in tables 2, 7 and 9, do not necessarily represent the typical conditions. This is due to the facts that the growth processes of the macaque vary individually to a very marked degree and that for many age periods only a few animals could be examined so far. Whenever possible a macaque, born in the Carnegie Colony, was weighed, measured and examined at weekly intervals during the first month, every two weeks during the next two months and once a month thereafter. Some of the animals, however, died from one cause or another at an early age, a few were needed for other investigations, and at certain times the author had to interrupt his regular examinations. For these reasons the number of specimens differs in different age periods, and is at present still much smaller in the late than in the early stages of growth. The data to be presented will serve, nevertheless, as a basis for the estimation of the age of animals with unknown date of birth, and for comparing the amount and kind of change occurring during a given period of growth in rhesus macaques of unknown age with the corresponding changes, shown by the following tables.

The technique of measuring the outer body of living or dead primates, the measurements themselves, and the proportions calculated from these measurements have been described in detail in a special paper by the writer (1929).

The only available fetus of known age is a specimen of *Macaca mulatta*, 75 (±2) days old and weighing 69 g. (preserved, 76 g.). This specimen is as yet entirely unpigmented and almost bare of hair, only the eyebrows, upper lip and chin showing a few colorless hairs. The ischial callosities have already appeared, being quite conspicuous (for measurements and proportions of this fetus see tables 3 and 4). Since the average duration of pregnancy in the rhesus macaque amounts to 164 days (Hartman, 1932; 30 cases), the above fetus had not yet reached the middle of intrauterine life.

TABLE 1

Sex and weight of the newborn, together with known duration of pregnancy

DURATION OF PREGNANCY	WEIGHT AT BIRTH	SEX
days	*grams*	
146	330	♀
147	380	♂
152	370	♂
163	430	♀
167	530	♀
169	450	♂
169	550	♀
171	440	♂
173	430	♀
178	600	♂
180	530	♂

The newborn rhesus macaque weighs anywhere from 330 to 600 grams, according to the records on 12 male and 12 female living newborns. The average weight of the males amounts to 438 g. and that of the females to 432 g. The sitting height (from vertex to ischial callosities, measured with sliding compass) varies in the same series of newborns between 168 and 207 mm. and averages 188 mm. in males and 190 mm. in females. The weight of the newborn macaque amounts to anywhere from about 6 to 10 per cent of the weight of its mother when not pregnant, this proportion being usually somewhat higher in small mothers than in large ones. As shown by the figures in table 1, the weight at birth is partly dependent upon the length of the prenatal period, premature babies being less heavy than those born after a pregnancy of normal or unusually long duration. Many of the former can gradually overcome their initial deficiency. For instance, female No. 97 weighed at birth only 330 g. and its sitting height measured only 168 mm. Female No. 73, on the other hand, had a birth weight of 530 g. and an accompanying sitting height of 188 mm. At the age of 19 months the weight of the former had increased to 1,770 g., whereas that of the latter to only 1,650 g., and the sitting height of the former had grown to 318 mm. and that of the latter to 329 mm.

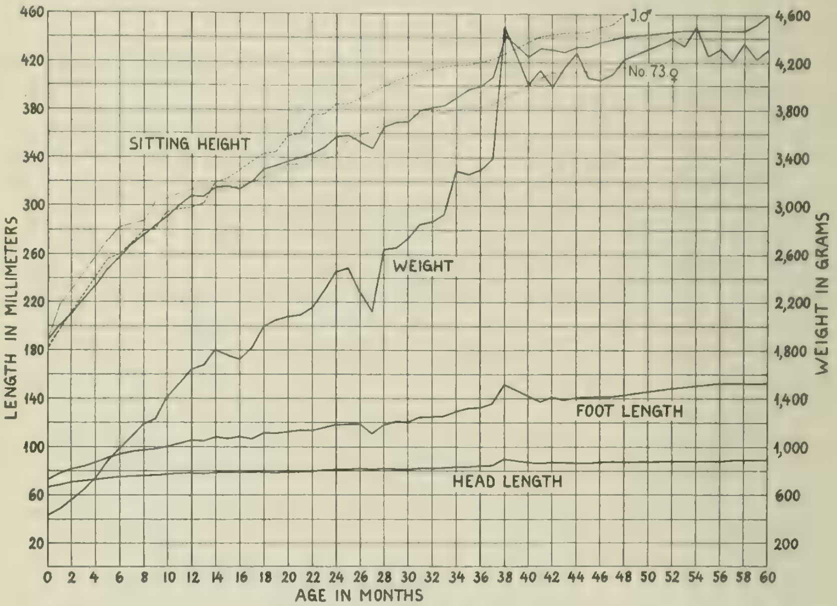

FIG. 2. Growth curves for sitting height, weight, foot length and head length of animals of known age, constructed from averages (cf. table 2). The broken (J, ♂) and the dotted (No. 73, ♀) curves show the *individual* growth in sitting height in two of the animals.

A premature birth may not only decrease the general size of the newborn baby, but may also cause an apparent retardation in various other growth processes. For instance, in a male (No. H), born on the 147th day of pregnancy, the great fontanelle was still open (greatest diameter 6 mm.), whereas normally it can not be palpated in newborn macaques. In the same specimen the first deciduous teeth (central incisors) did not erupt until the unusually late age of five weeks. Incidentally, this animal, though born prematurely, is still living at the age of five years and has always been in excellent health. On the other hand, in a male

TABLE 2

Tentative averages of body weight, sitting height, foot length and head length of animals of known age. Also the ranges of individual variations in sitting height

AGE	SPECIMENS	WEIGHT	SITTING HEIGHT			FOOT LENGTH	HEAD LENGTH
			Average	Minimum	Maximum		
months		*grams*	*mm.*	*mm.*	*mm.*	*mm.*	*mm.*
0	19	436	188	168	207	73	66
0.5	13	481	199	186	217	77	68
1	15	489	201	172	218	78	69
2	10	564	211	195	232	81	71
3	9	644	223	204	247	84	72
4	13	747	235	208	258	87	73
5	17	886	248	213	273	91	74
6	15	997	259	237	283	94	75
7	13	1,089	268	250	286	96	76
8	12	1,193	276	253	311	98	76
9	12	1,228	283	260	320	99	76
10	10	1,405	292	265	322	100	77
11	9	1,527	300	269	340	103	78
12	8	1,646	307	269	342	105	79
14	6	1,800	315	300	322	107	79
16	2	1,725	314	311	316	108	79
18	7	1,996	330	316	350	111	79
20	8	2,082	336	318	358	112	79
22	8	2,149	344	320	377	114	80
24	6	2,450	357	324	386	118	80
27	2	2,120	348	347	348	111	81
30	5	2,728	369	348	406	120	81
33	8	2,932	383	353	417	125	82
36	7	3,307	400	360	441	132	84
40	2	4,010	425	407	442	143	87
44	4	4,280	432	411	462	141	87
48	4	4,227	441	416	473	143	88
52	1	4,400	445			149	88
56	1	4,310	446			152	88
60	1	4,310	460			152	89
79	1	7,490	499			146	99
92	1	9,050	508			146	99

(No. M), born on the 180th day of pregnancy, all four central incisors had erupted on the tenth day after birth.

As shown by table 2 and by figure 2, on an average the weight at birth becomes doubled at the age of five months and quadrupled at the age of fifteen months. At the end of the third year the weight is seven and a half times greater than at birth and at the end of the fourth year nearly ten times. In the male macaque (No. H) studied for the longest period, the weight increased in the first year by 1,300 g., or by 342 per cent of the birth weight (380 g.), during the second year the increase amounted to only 610 g., or to 36 per cent of the weight at the age of one year. In the third year the annual increase was 780 g., or 34 per cent of the initial weight, in the fourth year the corresponding figures are 850 g. or 28 per cent, and in the fifth year 390 g. or 10 per cent. It is seen that the annual relative increase diminishes with advancing age.

At all ages the body weight varies to a surprising degree. Among seventeen fully grown, female, not pregnant rhesus macaques, all of which have had offspring, the optimum body weight varies individually beween 4,370 and 10,310 grams. The average weight of this series amounts to 6,175 grams, a value which lies very considerably below the average weight of 9,152 grams of five fully grown male rhesus macaques. This sexual difference in size must develop comparatively late in growth, since it is in no way apparent during at least the first four years of life.

The sitting height increases from an average of 188 mm. at birth to as much as 542 mm. in fully grown males, i.e., to nearly three times the size of the newborn. The sitting height of the newborn becomes doubled in the middle of the third year. This measurement grows at the most rapid rate during the first month (percentage increase about 15), but still increases at a considerable rate during the second to sixth months (average monthly percentage increase 5.6). During the second half of the first year the average monthly increase has slowed down to 2.1 per cent, during the second year to even only 0.9 per cent, and during the third year to 1.0 per cent.

The length of the foot grows from an average of 73 mm. at birth to exactly twice this size in an animal six and a half years old. The foot, therefore, increases not nearly as rapidly or as much as the sitting height, and the foot length varies individually less extensively than the sitting height.

The length of the head grows even more slowly than that of the foot, as is clearly shown by the curves in figure 2. From an average of 66 mm. at birth the head length has increased by only 50 per cent in an animal, six and a half years old, with a head length of 99 mm.

The estimation of the age of a rhesus macaque with unknown date of

TABLE 3

The most important dimensions of the outer body (in mm.) in animals of different ages

NUMBER ACCORDING TO SCHULTZ 1929	MEASUREMENT	FETUS 75 DAYS ♂	FETUS APPROX-IMATELY 135 DAYS ♀	NEWBORN ♂	6 MONTHS ♂	1 YEAR ♂	FULLY GROWN ♂	TWELVE FULLY GROWN FEMALES		
								Average	Minimum	Maximum
m 1	Sitting height	110	160	201	263	344	542	499	472	531
m 4	Tail length	44	91	108	138	172	249	224	189	261
m 5	Trunk height	56	83	108	159	230	346	334	305	351
m 14	Chest circumference	89	128	150	167	250	379	334	306	382
m 12	Chest breadth	26	36.5	41	46	75	101	92	84	100
m 13	Chest depth	27	36.5	47	50	80	116	104	92	114
m 9	Shoulder breadth	27	41	48	60	81	124	108	95	132
m 10	Hip breadth	21	34	41	53	77	118	109	100	117
m 47	Total lower limb length	51.5	90.5	124	168	229	349	334	313	356
m 15	Thigh length	25.5	43	60	84	111	172	166	157	178
m 17	Leg length	22	39	54	75	102	158	149	138	161
m 18	Foot length	25	54	72	92	112	156	148	138	154
m 48	Total upper limb length	64.1	118	154	199	250	395	376	352	407
m 21	Upper arm length	24.5	42	55	73	95	148	144	133	156
m 22	Forearm length	21.6	38	52	70	88	146	136	128	147
m 23	Hand length	18	38	47	56	67	101	95	87	105
m 26	Head length	37	57	66	76	85	104	89	80	95
m 28	Head breadth	35	47	51	60	67	87	71	64	78
m 31	Head height	23	38	38	42	43	52	45	39	50
m 49	Average head diameter	31.7	47.3	51.7	59.3	64.7	81	68.3	61	73.3
m 33	Total face height	17.5	25	33	40	45	77	64	54	72
m 30	Face breadth	33	39	46	54	64	87	79	68	86

TABLE 4

The most important body proportions in the same animals used in table 3

NUMBER ACCORDING TO SCHULTZ 1929	PERCENTAGE RELATION	FETUS 75 DAYS ♂	FETUS APPROXIMATELY 135 DAYS ♀	NEWBORN ♂	6 MONTHS ♂	1 YEAR ♂	FULLY GROWN ♂	TWELVE FULLY GROWN FEMALES		
								Average	Minimum	Maximum
i 3	$\frac{\text{Chest circumference}}{\text{Trunk height}}$	158.8	154.2	138.8	105.0	108.7	109.5	100.0	90.8	114.7
i 5	$\frac{\text{Hip breadth}}{\text{Trunk height}}$	37.5	40.9	37.9	33.3	33.4	34.1	32.7	29.7	38.0
i 6	$\frac{\text{Hip breadth}}{\text{Shoulder breadth}}$	77.8	83.0	85.4	88.3	95.0	95.2	101.3	88.0	119.6
i 7	$\frac{\text{Chest breadth}}{\text{Chest depth}}$	96.3	100.0	87.2	92.0	93.7	87.1	88.7	83.6	94.2
i 12 a	$\frac{\text{Tail length}}{\text{Sitting height}}$	40.0	56.8	53.7	52.5	50.0	45.9	44.8	37.9	53.1
i 13	$\frac{\text{Total lower limb length}}{\text{Trunk height}}$	92.0	109.0	114.7	105.6	99.5	100.8	100.1	90.3	112.7
i 15 a	$\frac{\text{Foot length}}{\text{Total lower limb length}}$	48.5	59.7	58.0	54.7	48.9	44.7	44.4	41.3	48.2
i 18	$\frac{\text{Total upper limb length}}{\text{Trunk height}}$	114.3	142.2	142.5	125.0	108.6	114.1	112.5	101.0	124.8

i 22	$\frac{\text{Forearm length}}{\text{Upper arm length}}$	88.2	90.5	94.5	95.9	92.7	98.7	94.6	87.7	98.5
i 21	$\frac{\text{Hand length}}{\text{Total upper limb length}}$	28.1	32.2	30.5	28.2	26.8	25.6	25.3	24.1	27.0
i 26	$\frac{\text{Total upper limb length}}{\text{Total lower limb length}}$	124.5	130.3	124.1	118.3	109.1	113.0	112.4	108.0	115.5
i 31	$\frac{\text{Average head diameter}}{\text{Trunk height}}$	56.6	57.0	47.8	37.3	28.1	23.4	20.5	18.6	23.4
i 32	$\frac{\text{Head breadth}}{\text{Head length}}$	94.6	82.5	77.2	78.9	78.8	83.6	80.3	76.5	84.7
i 35	$\frac{\text{Total face height}}{\text{Trunk height}}$	31.3	30.1	30.5	25.1	19.6	22.2	19.2	16.5	21.3
i 37 a	$\frac{\text{Total face height}}{\text{Average head diameter}}$	55.2	52.9	63.8	67.4	69.6	95.0	94.0	85.3	102.8

birth should be based not upon the variable weight or sitting height alone, but upon weight *and* several dimensions, as for instance those listed in table 2, in combination with the state of the dentition of the animal (see tables 7 and 9).

Table 3 contains the values for other bodily dimensions at various ages, including those of two fetuses. As shown by the indices, given in table 4, differing rates of growth of different parts of the body cause the proportions between measurements to change with advancing age. This is very striking, for instance, in the percentage relation between the average head diameter and the trunk height, which amounts to 57 in the two fetuses, to 48 in a newborn, to 37 in an animal six months old, to 28 in another animal one year old, and to only 23 in a fully grown male. According to these figures, the trunk grows much more intensively than the head. That the limbs grow faster than the trunk before birth, but more slowly than the trunk during postnatal life, is demonstrated by the proportions between the total limb lengths and the trunk height. In a newborn rhesus macaque the upper limb measures 143 per cent of the trunk height and the lower limb 115 per cent; in an adult male these percentages have decreased to 114 and to 101 respectively. These figures indicate also that the ontogenetic decrease in relative limb length is more pronounced in the upper than in the lower limb. The same conclusion is reached from the growth changes in the direct proportion between the lengths of the upper and of the lower limb. The former length amounts to 124 per cent of the latter length at birth, but to only 113 per cent in adult life.

TABLE 5

Tail length in percentage of sitting height at different ages in six living animals

AGE	NUMBER					
	H, ♂	J, ♂	72, ♀	73, ♀	76, ♀	97, ♀
Birth	61.3	59.6	55.2	60.1	59.3	63.1
6 months	55.9	58.0	52.8	54.1	59.4	59.5
12 months	52.8	55.1	48.7	51.9	52.1	55.4
24 months	51.2	49.7	46.4	50.9	51.8	53.4
36 months	51.8	51.6	46.9	50.3	53.2	51.9
48 months	52.4	52.2		51.9	54.1	
60 months	52.2					

Table 5 demonstrates by the individual growth changes in a few specimens that the length of the tail grows in general more slowly than the sitting height, since the proportion between these two measurements decreases with advance in age. In adult rhesus macaques the tail length averages only 45 per cent of the sitting height.

Some body proportions undergo comparatively little change in the course of postnatal development. As shown by the examples in table 6, the breadth of the head in relation to the length increases somewhat during the first month, but the changes in this index during at least the subsequent three years are in most cases quite insignificant. Only in the most dolichocephalic specimen (G) does the head breadth continue to grow considerably faster than the head length, so that at the end of three years its relative head breath has become equal to that in the other animals. The late and striking postnatal increase of this proportion in the powerful male (B) with full permanent dentition is probably caused entirely by the excessive development of its temporal muscles.

TABLE 6

Head breadth in percentage of head length at different ages in seven living animals

AGE	NUMBER						
	G, ♂	J, ♂	H, ♂	B, ♂	72, ♀	73, ♀	76, ♀
Birth	71.8	77.8	78.4	....	77.9	77.3	75.7
1 month	73.6	79.5	80.9	....	81.9	80.4	78.4
6 months	73.8	80.0	81.3	....	79.5	81.3	78.7
12 months	75.0	79.5	81.0	....	79.0	81.6	78.2
24 months		79.5	81.5	....	81.5	81.8	81.1
36 months	82.2	79.7	81.5	....	81.7	83.5	82.5
48 months		80.0	81.6	....		84.1	82.4
60 months			82.0	....			
79 months				85.9			
92 months				89.9			

Tables 3 and 4 give the measurements and some of the more important proportions of one large adult male and the averages and ranges of variations of the same absolute and relative measurements of twelve adult females. These data show clearly the extent to which perfectly normal individuals can differ from one another and that, on account of this variability, it is impossible to demonstrate many significant secondary sex differences in body proportions. The only instance in which an index of the male falls considerably outside the range of variations in the same index of females is found in the relation between the height of the face and that of the trunk. According to this proportion male rhesus macaques have the relatively larger face, undoubtedly in consequence of the larger dentition in males than in females. In regard to eleven out of the twenty-two absolute measurements in table 3 the male surpasses the maximum variations among the females.

For the estimation of the age of young rhesus macaques with unknown date of birth observations on the dentition[1] are of great assistance in addition to a consideration of the weight, sitting height, etc., of the animals. The author's records of the ages at which the various teeth erupt in rhesus monkeys, born in captivity, are listed in a condensed form in tables 7 to 9. The age of eruption refers here not to the time when the first, small, white tip of a tooth appears through the gum, but rather to the time when the entire top of the crown has just pierced the gum, though the tooth is still far from functioning by meeting its antagonist in the other jaw. Again it should be emphatically stated that the averages, given in the tables, can be regarded as merely tentative figures, based upon relatively few observations of an extremely variable process. This variability is evident from the following examples: The age of eruption of the first teeth to appear, the lower middle incisors, varies among 18 animals between 2 and 35 days after birth. The age of eruption of the last deciduous tooth, the upper second molar, varies among 13 animals between 16 and 32 weeks, the minimum being quite exceptional, since ten cases vary only between 23 and 29 weeks. The appearance of the first permanent tooth, the lower first Molar, occurs among 9 animals anywhere between the eighteenth and the twenty-fourth month.

According to the averages in the tables, all of the incisors erupt in general during the first six weeks, the canines and first molars are added during the twelfth to fourteenth weeks, and the second molars during the twenty-third to twenty-fifth weeks. After the complete eruption of the deciduous set of teeth during the first six months of postnatal growth, there occurs a pause of, on an average, fourteen months until the eruption of the permanent teeth begins in the twentieth month with the lower first Molars. The latter are followed one month later by the upper first Molars. From twenty-one to thirty-one months the dentition remains on an average unchanged. The permanent Incisors make their appearance during the thirty-first to thirty-eighth months and are followed by the second Molars in the forty-second month. After the eruption of the second Molars there seems to occur a brief period of rest before the Premolars and Canines are added to the permanent dentition, and this in rather irregular and rapid (46 to 49 months) succession. Judging by the records on only one animal, the last permanent teeth, the third Molars, do not erupt until after a surprisingly long interval. In this perfectly normal and healthy male rhesus macaque the lower third Molars appeared at the age of six and a half years and the upper third Molars not until the age of seven and a half years. It is interesting to note that in the rhesus macaque the deciduous dentition is complete at the age of six months, when the milk teeth are just beginning to appear in man, and that the permanent dentition of the rhesus macaque becomes completed during the eighth year, or only one year after the average age at which the first permanent teeth erupt in man.

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[1] In comparing the data on the eruption of the teeth as presented in this chapter with those in chapter VI the reader will note a considerable disparity. This is, however, more apparent than real, and is due to the differences in methods and definitions of eruption employed by the two contributors. Dr. Schultz made monthly examinations of the growing members of the Carnegie monkey colony (see table of births in Hartman, Contributions to Embryology, 1932, p. 52), recording the eruption of a given tooth when this had clearly emerged from the gum. Dr. Marshall used x-ray evidence and defines eruption as emergence from the jaw-bone. He also studied radiologically as well as histologically the jaws of some of the young animals of the colony that died. The figures in chapter VI are, therefore, as is to be expected, consistently lower than those of chapter II. Both kinds of data are important and useful. The *order of eruption* may vary somewhat in individual cases; but the norm would seem to be clearly established from 419 skulls reported upon in this chapter.—(The editors).

TABLE 7

Tentative averages of the age (in weeks) and sequence of eruption of the deciduous teeth in animals of known age

SEQUENCE	DECIDUOUS TOOTH	SPECIMENS	AGE OF ERUPTION		
			Average	Minimum	Maximum
1	Lower middle incisor	18	2.8	0	5
2	Upper middle incisor	17	2.9	1	5
3	Lower lateral incisor	15	4.3	2	7
4	Upper lateral incisor	14	6.0	3	7
5	Upper canine	10	12.4	8	16
6	Lower first molar	10	13.4	8	18
7	Lower canine	10	14.0	8	17
8	Upper first molar	10	14.2	10	19
9	Lower second molar	15	23.0	15	29
10	Upper second molar	13	25.2	16	32

The sequence of eruption of the permanent teeth, as obtained in the

TABLE 8

The age of eruption (in months) of the permanent teeth in animals of known age

Deciduous teeth = *i* (incisor), *c* (canine), *m* (molar); permanent teeth = I (Incisor), C (Canine), P (Premolar), M (Molar); ? = tooth has not yet appeared at maximum age observed.

NUMBER	SEX	MAXIMUM AGE OBSERVED	UPPER JAW								LOWER JAW							
			I_1	I_2	C	P_1	P_2	M_1	M_2	M_3	I_1	I_2	C	P_1	P_2	M_1	M_2	M_3
		months																
X	♂	34	*i*	*i*	*c*	*m*	*m*	22	?	?	*i*	*i*	*c*	*m*	*m*	20	?	?
G	♂	42	34	40	*c*	*m*	*m*	24	39	?	35	41	*c*	*m*	*m*	24	38	?
J	♂	49	27	39	*c*	48	46	20	42	?	27	33	*c*	49	48	18	41	?
H	♂	60	36	38	*c*	57	56	23	48	?	36	38	—	*m*	59	22	51	?
B	♂	92	I	I	C	P	P	M	M	90	I	I	C	P	P	M	M	79
65′	♀	35	35	*i*	*c*	*m*	*m*	21	?	?	34	*i*	*c*	*m*	*m*	19	?	?
97	♀	37	34	37	*c*	*m*	*m*	20	?	?	32	34	*c*	*m*	*m*	19	?	?
72	♀	41	25	40	*c*	*m*	*m*	20	?	?	30	34	*c*	*m*	*m*	18	?	?
76	♀	48	27	38	47	48	*m*	21	43	?	36	38	44	*m*	48	20	42	?
73	♀	49	33	37	48	42	43	19	39	?	35	36	47	44	43	19	40	?

relatively few living macaques of known age, is confirmed by the author's examination of the dentitions in 419 macaque skulls,[2] listed in table 10. According to this series the permanent dentition begins with the lower first Molars. No case was found in which the upper first Molars erupted earlier than the lower ones, but the upper and lower ones may appear simultaneously in exceptional cases. The Incisors are the next teeth to be added to the permanent dentition, the middle ones appearing

TABLE 9

Tentative averages of the age (in months) and sequence of eruption of the permanent teeth, based upon the cases listed in table 8

SEQUENCE	PERMANENT TOOTH	SPECIMENS	AGE OF ERUPTION		
			Average	Minimum	Maximum
1	Lower first molar	9	20	18	24
2	Upper first molar	9	21	19	24
3	Upper middle incisor	8	31	25	36
4	Lower middle incisor	8	33	27	36
5	Lower lateral incisor	7	36	33	41
6	Upper lateral incisor	7	38	37	40
7	Lower second molar	5	42	38	51
8	Upper second molar	5	42	39	48
9	Lower canine	2	46	44	47
10	Lower first premolar	2	47	44	49
11	Upper second premolar	3	48	43	56
12	Upper canine	2	48	47	48
13	Upper first premolar	4	49	42	57
14	Lower second premolar	4	49	43	59
15	Lower third molar	1	79		
16	Upper third molar	1	90		

---

[2] Two hundred and thirty-nine of these skulls belong to the U. S. National Museum and the remaining 180 skulls are in the Anatomical Department of the Johns Hopkins University. Two hundred and fifteen skulls are from wild-shot animals and 204 from captive specimens. Many different species are represented; of the rhesus macaque there are 149 individuals. Captivity does not in any way influence the sequence of tooth eruption; most of the "exceptions," listed in table 10, are from wild-shot specimens. No species differences could be detected in regard to the sequence of eruption. From the data available at present it seems possible, though not yet certain, that the permanent Canines tend to erupt slightly later in male than in female macaques.

TABLE 10

The dental formulae of 419 macaque skulls with at least part of the permanent dentition

For explanation of the letters in the dental formulae see table 8.

NUMBER OF SKULLS	DENTAL FORMULA	REMARKS REGARDING INCOMPLETE ERUPTION	EXCEPTIONS (SINGLE CASES)
11	$\frac{i\ i\ c\ m\ m}{i\ i\ c\ m\ m\ \mathrm{M}}$	In 6 cases lower M_1 not fully erupted	
46	$\frac{i\ i\ c\ m\ m\ \mathrm{M}}{i\ i\ c\ m\ m\ \mathrm{M}}$	In 11 cases upper M_1 not fully erupted	
4	$\frac{\mathrm{I}\ i\ c\ m\ m\ \mathrm{M}}{i\ i\ c\ m\ m\ \mathrm{M}}$		$\frac{i\ i\ c\ m\ m\ \mathrm{M}}{\mathrm{I}\ i\ c\ m\ m\ \mathrm{M}}$
11	$\frac{\mathrm{I}\ i\ c\ m\ m\ \mathrm{M}}{\mathrm{I}\ i\ c\ m\ m\ \mathrm{M}}$	In 3 cases upper i_2 lost	$\frac{i\ i\ c\ m\ m\ \mathrm{M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M}}$
12	$\frac{\mathrm{I}\ i\ c\ m\ m\ \mathrm{M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M}}$	In 8 cases lower I_2 not fully erupted; in 1 case upper i_2 lost	
9	$\frac{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M}}$	In 6 cases upper I_2 not fully erupted	
11	$\frac{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M}}$	In 8 cases lower M_2 not fully erupted; in 5 cases upper I_2 not fully erupted	$\frac{\mathrm{I}\ i\ c\ m\ m\ \mathrm{M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M}}$
13	$\frac{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M}}$	In 8 cases upper M_2 not fully erupted; in 1 case upper I_2 not fully erupted	$\frac{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M\ M}}$
3	$\frac{\mathrm{I\ I}\ c\ \mathrm{P}\ m\ \mathrm{M\ M}}{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M}}$	In 3 cases upper P_1 not fully erupted	$\frac{\mathrm{I\ I}\ c\ \mathrm{P}\ m\ \mathrm{M\ M}}{\mathrm{I\ I}\ c\ \mathrm{P}\ m\ \mathrm{M\ M}}$
6	$\frac{\mathrm{I\ I}\ c\ \mathrm{P}\ m\ \mathrm{M\ M}}{\mathrm{I\ I\ C}\ m\ m\ \mathrm{M\ M}}$	In 5 cases lower C not fully erupted; in 4 cases upper P_1 not fully erupted	$\frac{\mathrm{I\ I}\ c\ \mathrm{P}\ m\ \mathrm{M\ M}}{\mathrm{I\ I\ C}\ m\ \mathrm{P\ M\ M}}$
2	$\frac{\mathrm{I\ I}\ c\ m\ m\ \mathrm{M\ M}}{\mathrm{I\ I\ C\ P}\ m\ \mathrm{M\ M}}$	In 2 cases lower C not fully erupted; in 1 case upper M_2 not fully erupted	$\frac{\mathrm{I\ I}\ c\ \mathrm{P}\ m\ \mathrm{M\ M}}{\mathrm{I\ I\ C\ P}\ m\ \mathrm{M\ M}}$
2	$\frac{\mathrm{I\ I}\ c\ m\ \mathrm{P\ M\ M}}{\mathrm{I\ I}\ c\ m\ \mathrm{P\ M\ M}}$	In 1 case upper and lower P_2 not fully erupted	
5	$\frac{\mathrm{I\ I}\ c\ \mathrm{P\ P\ M\ M}}{\mathrm{I\ I}\ c\ m\ \mathrm{P\ M\ M}}$	In 2 cases lower *c* lost	
4	$\frac{\mathrm{I\ I}\ c\ \mathrm{P\ P\ M\ M}}{\mathrm{I\ I\ C\ P\ P\ M\ M}}$	In 4 cases lower C not fully erupted; in 2 cases upper *c* lost	
2	$\frac{\mathrm{I\ I\ C\ P}\ m\ \mathrm{M\ M}}{\mathrm{I\ I\ C\ P\ P\ M\ M}}$	In 2 cases all C and P not fully erupted	$\frac{\mathrm{I\ I\ C\ P\ P\ M\ M}}{\mathrm{I\ I\ C\ P}\ m\ \mathrm{M\ M}}$
30	$\frac{\mathrm{I\ I\ C\ P\ P\ M\ M}}{\mathrm{I\ I\ C\ P\ P\ M\ M}}$	In 13 cases upper C not fully erupted; in 9 of these cases lower C not fully erupted	
21	$\frac{\mathrm{I\ I\ C\ P\ P\ M\ M}}{\mathrm{I\ I\ C\ P\ P\ M\ M\ M}}$	In 8 cases upper C not fully erupted; in 9 cases lower M_3 not fully erupted	
219	$\frac{\mathrm{I\ I\ C\ P\ P\ M\ M\ M}}{\mathrm{I\ I\ C\ P\ P\ M\ M\ M}}$	In 5 cases upper M_3 not fully erupted; in 2 of these cases upper C not fully erupted	

before the lateral ones. The third period in the formation of the permanent dentition is represented by the eruption of the second Molars, which invariably precedes the appearance of any of the Premolars and Canines. According to all the data in tables 9 and 10, both the lower and the upper second Molars are always present before any Premolar has replaced a deciduous molar. This finding is not in agreement with the statement by Krogman (1930), that in "*Pithecus rhesus*" all the Premolars erupt sooner than the second Molars. As has already been stated above in regard to the macaques of known age, the fourth period in the eruption of the permanent teeth is very irregular. The data in table 10 show this very clearly by the lack of uniformity in the sequence of eruption of the Premolars and Canines. In living macaques it has been repeatedly noticed that the deciduous molars can be retained more or less loosely for a very considerable period before they are shed, apparently being held in place mostly by the gums. In carefully prepared skulls it can be seen that such deciduous molars merely straddle the crown of the replacing Premolars, which may already reach well above the alveolar margin. For this reason the Premolars appear in most cases immediately after the milk molars have actually fallen out. The last phase in the formation of the permanent dentition consists in the appearance of first the lower and afterwards the upper third Molars.

Among the 200 macaque skulls with the permanent dentition started, but not completed, not one single case was found in which either the synchondrosis spheno-occipitalis or the sagittal suture was closed. The latter apparently never become obliterated until some time after all the teeth have fully erupted.

With advancing age the teeth show signs of attrition due to prolonged usage. Such "grinding-off" is noticed first on the upper middle Incisors and slightly later on all the other Incisors. Signs of wear appear next on the Canines (particularly in males) and on the first Molars. These are followed by the second Molars, then by the Premolars and last of all by the third Molars. In very old animals all the teeth may become worn down to the gums, the Incisors and first Molars usually showing this process first and in the most extreme degree. Among wild as well as captive macaques specimens are occasionally found which demonstrate clearly that these animals can outlive their dentitions, since most of their teeth are represented by mere stumps or may even have become lost altogether. That such animals are probably considerably over twenty years old is indicated by the following two cases in the Johns Hopkins collection of primates: (1) a large female macaque, having lived for slightly over twenty years in captivity and having been captured "when young," shows a complete dentition with marked, but not yet extreme, wear of of the teeth; (2) a male macaque, weighing over ten kilograms, died following a fight with several male cage mates in the twenty-fourth year of captivity. This animal, when received at the zoological garden, was considered to have been fully grown. At death its dentition was found to be but moderately worn, the Incisors and Canines showing considerable wear, but the Premolars and third Molars practically none. In this specimen all of the cranial sutures and all epiphyseal lines are obliterated.

Finally, a few data are added here to show, at least tentatively, the age of sexual maturity in the rhesus monkey. In one male (G) of known age the left testis descended into the scrotum at the age of 34 months and the right one two months later, but at the age of 38 months both testes were back in the canal, where they still were at the last examination at 43 months. In another animal (J) the testes had never descended during the first four years. In a third animal (H) the right testis descended into the scrotum at the age of 52 months, but one month later returned into the canal, where both testes still were at the beginning of the sixth year. The permanent descent apparently does not take place before the middle of the sixth year. According to Hartman (1932) the first sperms were seen in one male rhesus macaque (B) at the age of 41 months; the first impregnation by the same animal occurred at the age of 54 months. It may be mentioned in this connection that the permanent dentition of this same macaque was not complete until the age of 90 months.

The female rhesus macaque does not seem to menstruate until the beginning of the fourth year. The first menstruation was recorded in two animals of known age when they were 36 months (No. 76) and 37 months (No. 73) old. Hartman (1932) reports the weights and sitting heights of fifteen macaques at the time of their first menstruation; from these data it can be estimated by means of table 2 that the animals were on an average about 37 months old. Also according to Hartman nine female macaques had reached an average weight of approximately 5,000 grams at their first conception. Such a weight is acquired at the earliest during the sixth year, i.e., long after the first menstruation. Hartman mentions one animal, for which it is known that menstruation continued to an age of not less than fourteen years.

These observations on the growth of the rhesus macaque are unfortunately still quite fragmentary. Nevertheless it can be stated definitely that all the developmental changes proceed very much more rapidly in the macaque than in the higher primates, particularly man. The macaque, however, does not grow quite as rapidly as has been claimed by a number of authors. Pronounced individual variations in rate of growth are very common among macaques.

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CHAPTER III

THE SKIN AND ITS APPENDAGES

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SKIN

Pigmentation. A variable distribution of pigment cells, limited almost entirely to the deeper layers of the corium, gives the general color effect of a pale tint of blue. Though the relative tone is made out with difficulty over the dorsal surfaces where the hair is most dense, the color is usually light and mottled on the back, becoming uniformly dark on the distal portions of the extremities and tail. The blue coloration is readily visible over the ventral surfaces, and here in contrast are several sharply defined unpigmented areas, somewhat constant in position, but varying in size. Such unpigmented areas, which include the anterior neck, axilla and medial side of the arm, inguinal region and medial side of the thigh, appear in life as a delicate pink. The upper eyelids are unpigmented, while the other parts of the face, including the ears, have only a trace of blue, appearing in life as a dusky pink.

Palms and soles. (See chapter IV.)

Interdigital webbing (fig. 8). There exists practically no webbing between any of the fingers. Between the toes, however, true cutaneous webbing is present. This is most pronounced between the second and third digits. Here it usually reaches to the distal end of basal phalanx II or to the middle of middle phalanx II, or in rare instances even to the distal end of middle phalanx II. Between toes III and IV and toes IV and V the webbing usually extends only to the middle of the basal phalanges, but occasionally may reach the proximal interphalangeal joints.

Callosities (fig. 77). Two well defined cornified pads overlie the ischial tuberosities and vary in shape from ovoid to reniform. In the female the inferomedial ends of the callosities are separated by the vulva (fig. 77), while in the male the same are closely approximate (fig. 70). The resulting angle, formed by the long axes of the two callosities, averages about 90°. The color varies from yellow to red, depending on the stage of the sexual cycle.

The sexual skin. The adult sexually active rhesus monkey presents a marked reddening of the skin about the genitalia and over the buttocks. This region, called the "sexual skin," is to a degree under the influence of the autonomic nervous system (Langley and Sherrington). The color is more limited in extent in the male than in the female; in the latter it passes some distance up the back, about as high as the crest of the ilium. The area is usually delimited in a definite line across the middle of the thigh, but at times may pass in red splotches down the legs to the heel and in a median streak on the belly from the symphysis to the umbilicus. Ventrally the sexual skin is visible in a triangular area over the symphysis. In younger females the reddening of the sexual skin is most marked at the middle of the menstrual cycle, blanching out considerably with the approach of the menstrual flow. Old animals in good health are, however, chronically red, with little cyclic variation. Animals are more brilliant when exposed to sunlight. The reddening is due to engorgement of a plexus of especially large, thin-walled blood vessels beneath the epithelium, and is not due to pigmentation (Collings), nor is it inflammatory in nature.

At times the reddening may be accompanied by swellings, which in adolescents may reach almost pathological proportions. The swellings may cover the whole sexual skin area, including the base of the tail, which is thrown into enormous folds or rugae, and may even invade the dorsal surface of the flanks and the thighs and crura. In other instances the swellings are confined to the margins of the sexual skin. The most marked swellings characterize young females three or four to five years old; they are rare in multiparae, having been seen in only two or three of many old females of the Carnegie Colony. In young females the most pronounced swellings often occur in the "scrotal" region over the symphysis, a region homologous to the scrotum of the male (cf. chapter XI).

HAIR

Distribution and character. Except for the upper eyelids, nipples, callosities, palms, soles, and terminal phalanges, the body is covered with straight hair of a texture generally medium, though varying somewhat with density, that is, slightly coarser, on the scalp and dorsal surfaces.

Density. Hair of maximum density appears on the scalp, with the hair of the back slightly thinner, and that on the chest and abdomen about one-tenth as thick as on the scalp. Thinner still is the hair of the genital and anal regions. The hair of the dorsal and ventral sides of the extremities have densities approaching those of the back and belly, respectively. On the face the hair is moderately dense, while that on the ear, with the exception of the tragus, is very scanty.

It should be pointed out that in the spring of the year rhesus monkeys shed their hair, sometimes completely. Hence at this time the animals present a most unprepossessing appearance. Several months are required to grow the new season's pelt.

Length. Hair length varies in different individuals, some having rather shaggy coats. However, maximum length usually occurs over the upper back, with the hair of the chest and lower parts of the trunk coming next, followed by that of the head and extremities. The shortest hair occurs about the nose and on the ear.

Color. The general color effect is dependent upon the fact that the individual hair shafts are not uniformly pigmented. Thus over the upper back and head the proximal half of the shaft is a "hair brown" (Ridgway's Color Standards), while the distal half is banded with black and yellow ochre, the total effect being that of bister. Over the lower back the apical half may vary from a yellow ochre to an ochraceous orange, black tipped, with an effect varying from buckthorn brown to hazel or even rufous. On the dorsal surface of the upper extremity the hair brown shaft is banded apically with buff, giving the effect of an olive brown. The dorsal surfaces of the lower extremities and tail partake of the color of the back, though with less orange, and the tail somewhat the darker.

All ventral surfaces are light, varying from pale to deep olive buff.

Directions. Figures 3 and 4 illustrate, semi-diagrammatically, the hair directions in a female fetus (no. 141, Johns Hopkins Anatomical Laboratory) of 163 mm. crown-rump length. The directions on this specimen may be considered as fairly representative of the group. The following variations, however, have been observed: (1) Occasionally a crest is found replacing the cheek whorl, in which case the crest is directed diagonally upward and backward from the mouth to the ear, and thus the divergence point at the anterior incisure of the ear is eliminated. (2) A simple midline divergence point is rather common on the upper chest, but single and double whorls are also possible. When double, the right whorl is counter-clockwise, the left clockwise. (3) A simple convergence point, rather than a whorl, may be present near the elbow. (4) All whorls and crosses may vary in relative position.

Sinus hairs. These are limited to three positions: The supra-orbital margin, upper and lower lips. In the adult it is impossible to define the limits of the sinus hairs without histological and embryological assistance, the resemblance to true head hair being so marked. The longest hairs of the supra-orbital margin are found along the medial half, are stiff and black, and may reach a maximum length of 3 cm.; they are directed

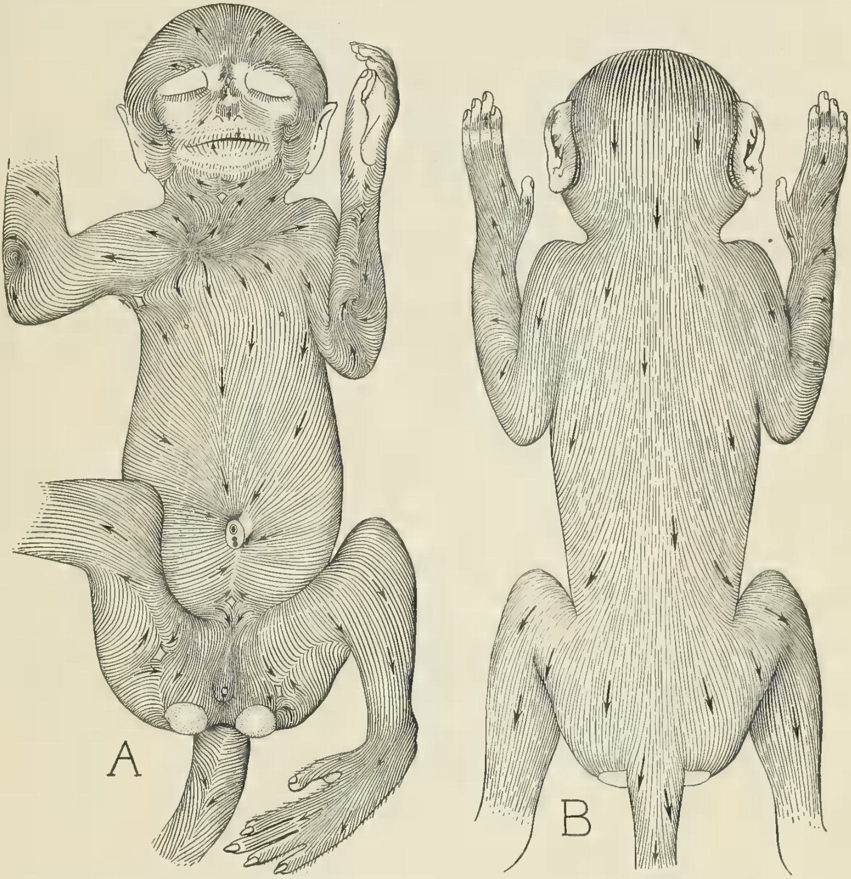

Fig. 3. Two views of female fetus (J. H. Anat. Lab. No. 141), 163 mm. C. R. length, showing approximate hair direction.

forward and upward. The longest hairs of the upper lip occur laterally, are black, but not quite as stiff as those on the supra-orbital border; they tend to curve forward and downward, reaching a maximum length somewhat exceeding 2 cm. Lighter hairs of the same length as those on the upper lip, but varying in direction, are scattered for some distance below the mouth. Short hairs immediately below the mouth tend to curve upward. No row-formation is observable in any of the regions.

NAILS

Curvature. Figure 5 shows the curvatures, both in longitudinal and cross sections, of representative finger and toe nails. The nails of the thumb and great toe show marked differences in curvature from those of the other fingers and toes, while the latter do not vary greatly among themselves.

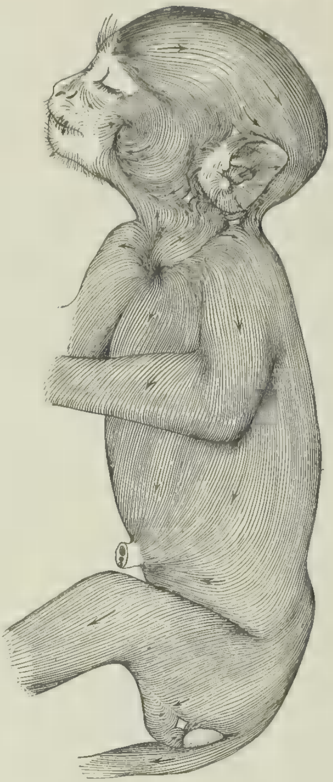

FIG. 4. Side view of same specimen shown in figure 3.

Size. The nail of the great toe is always both broader and longer than that of the thumb; that of the second toe on the average is slightly narrower than that of the second finger; and each of the three remaining toe nails has about the same width as the corresponding finger nails, but the third nail of both sets is always somewhat wider than either the second or fourth, and the fifth nail is the narrowest of both sets. Length is a variable feature depending on wear, but in general the toe nails are the longer.

Lunula. This is not visible.

Ridges. On the surface of each nail are a variable number of longitudinal, and sometimes also diagonal, ridges. It seems likely that the formation of these ridges is influenced by such factors as diet and disease and hence too much significance should probably not be attached to their number or arrangement.

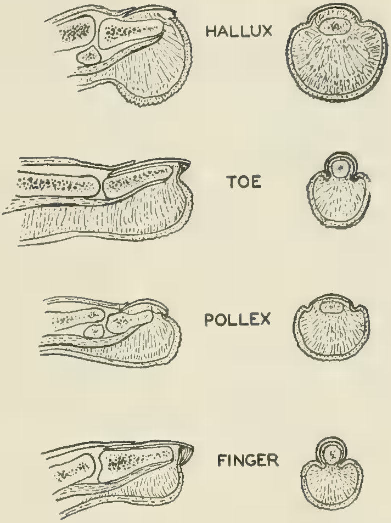

Fig. 5. Longitudinal and transverse sections of the distal portions of toes and fingers, to show the curvature of the nails.

Sole plate ("*Sohlenhorn*"). A fan-shaped development from the fleshy finger tip fills the concavity of the free margin of each nail and bears a continuation of the dermal-ridge pattern.

MAMMÆ

The following statements concern females primarily; the male breast resembles that of the non-menstruating virginal female.

Nipples. In adults the distance of the nipples above the symphysion represents about 82 per cent of the anterior trunk height (Schultz), a position corresponding to about the level at which the sixth rib joins the sternum. The two nipples are separated by a distance varying around 3 cm.

In adolescents, aged about 3 years, the nipples project only 4 or 5 mm., but during certain menstrual cycles may increase in length to 8 mm. as they become swollen and edematous in response to female sex hormone.

Nipple size in mature females depends very little on the size of the individual, much more on the endocrine state of the reproductive organs, most of all on parity, and especially on the time elapsed since nursing a baby. In the majority, nipple length varies between 9 and 12 mm.; diameter between 5 and 6 mm. However, multiparae are not always to be recognized by the size of their breasts, because after lactation ceases involution may continue even to the virginal state. Recently imported females, on the other hand, almost always possess enlarged nipples, since in a state of nature they are almost continuously nursing.

One notes at times a disparity in size of the two nipples. Thus among 65 mature females the right was markedly longer 5 times, the left 4 times; a slight disparity occurred 13 times, to the advantage of the right side 11 times. It is during lactation that the disparity is usually very marked, so that one nipple may be double the length of the other. This is due to the traction placed on the nipple by the baby.

Ducts. Situated on the tip of the nipple and just visible to the unaided eye are an inconstant number of duct openings, variably arranged; there may be only two or three ducts or as many as eight or ten, together with several minute "accessory" ducts; commonly there is a central duct within a circle of four or five.

Areolae. These are usually insignificant, and are as often indicated as not.

Both the areolae and the nipples undergo cyclic color changes similar to those of the sexual skin. Sometimes the reddened area may attain a considerable diameter, up to 20, 25 or even 30 mm. This is especially true of pregnancy and at times outside of pregnancy in old multiparae; but usually the areolae are reddened for a very narrow and always quite irregular zone. The colored area is often mottled and frequently contains visible gland openings.

Mammary glands. The gland tissue itself is so well spread out under the skin that it does not manifest itself externally except in lactation. The lactating gland extends laterally far into the axillary region and caudally may reach the costal border. Usually it is not possible to feel much growth of the mammae before the middle of pregnancy, and even at the end the thickening is not great; indeed, throughout successful nursing, since the baby keeps the milk well drained, the mammary tissue is hardly noticeable externally. Occasionally, however, the glands are very palpably enlarged, in rare instances so much so that they become pendulous and hang in large folds.

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Chapter IV

DERMATOGLYPHICS

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Among the most distinctive regional specializations of the integument is that characterizing the volar (palmar and plantar) surfaces. These areas are marked by a sculpturing of delicate ridges, assembled in configurational systems arranged according to a definite morphological plan. The systems of especial morphological importance are those associated with volar pads, such configurations being generally in the form of circumscribed patterns, commonly concentric whorls and loops (figs. 8 and 9). Suggesting as they do a finely engraved surface, the features of the ridged skin are collectively termed "dermatoglyphics." In here considering the dermatoglyphics attention is directed to the minute anatomy of the specialized integument, the morphological plan of the configurations, and the functional significance of ridges and their configurations.

MINUTE ANATOMY

Sepcialization of the volar skin is indicated not only by its ridged surface but also by hairlessness, absence of sebaceous glands, and increased number and size of sweat glands.

The detail of the surface markings is to be first examined. These features may be studied either by direct inspection of the skin or, with the advantage of sharper definition, in prints made by inking the surface and pressing it against white paper. Such a print is reproduced in figure 6, its tracery of lines and dots being impressions of the inked ridge summits.

It is obvious that the elevation of epidermal ridges (cristae cutis) has a correlate in a negative configuration of grooves (sulci cutis). The orifices of sweat glands are distributed in precise relation to the ridges; they are situated on the ridge summits, each ridge having a single row, with the pores regularly spaced. The ridges may be regarded as composed of segments, or structural units, a segment being that interval in which a sweat pore is centered. Occasionally, in the midst of literal

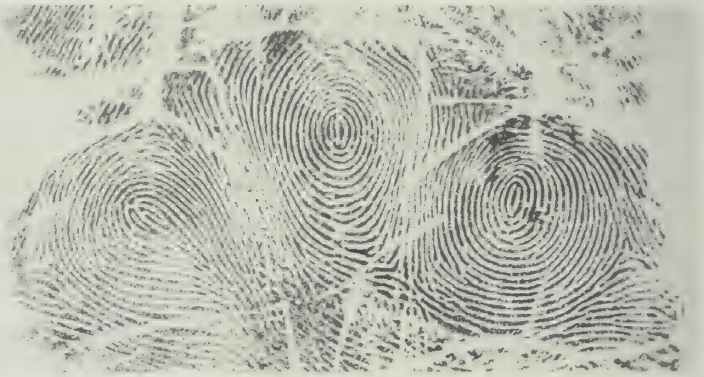

FIG. 6. Print of the distal region of the palm, with the second, third and fourth interdigital patterns, illustrating details of ridge construction. Being a contact print of the right palm, the anatomical relations are equivalent to the direct views illustrated in figures 8 and 9.

ridges, one of these ultimate structural units may occur independently, appearing as a discrete "island" bearing a single pore.

The texture of volar skin is not a uniform succession of continuous, parallel ridges. Instead, the ridges present local peculiarities in course associated with their construction of local dermatoglyphic systems. In addition to such major variations in the courses of ridges and the assembling of systems there are certain variations of individual ridges, known technically as *minutiae* or *Galton details*. If epidermal ridges were like the ribs of corduroy, parallel, straight and continuous, minutiae would not exist, for by definition they represent departures from such uniformity. Recalling that an island represents the segmental unit of ridge structure, minutiae may be descriptively defined, further, as irregularities in the linear consolidation of these units. Thus, one unit may exist independently; two, three of several units may be united to form a short ridge; greater numbers are represented in ridges of long course, yet even here it is common to find that the ridge is eventually abruptly terminated. Quantitative irregularity is therefore expressed as variations in ridge length. There is, besides, some variation in breadth of ridges. As illustrated in figure 8, certain regions have coarse ridges (e.g., the proximal portion of the vola) and others (e.g., the balls of the digits) bear finer ones. Directional irregularity appears not only in unlike courses of whole ridges, but also in branching, and it may be noted that the two ridges issuing from a branch may either continue singly or rejoin as a single ridge. Figure 6 provides ample demonstration of the diversity of ridges, as well as the large number of particular features which may be located in a relatively small territory. In addition to the variations above mentioned there is an important detail of ridge arrangement associated with the conjunction of systems having opposed directions. At a point where such systems meet there occurs a minute triangular aggregation of ridges known as a "triradius," or delta. Several triradii related to interdigital patterns are shown in figure 6.

Individual determatoglyphic variation reaches its maximum expression in the minutiae, so numerous are the variables concerned. While investigations of individual variations are almost limited to human dermatoglyphics, it may be taken for granted that *Macaca mulatta* offers no exception to the generalizations made for man. Certainly the statement may be made that no two individuals present duplicate configurations, and it is probable that the unlikeness holds true even for small homologous territories. The number and diversity of the ridge details are sufficient to indicate that the chance of duplication is reduced to a theoretical possibility so small as to be negligible.

The dermatoglyphic features apparent on the skin surface are correlated with the deeper organization of the integument. The epidermis is marked not only on the surface by ridges and sulci, but its inner configuration as well exhibits a constant association with the external features. The ridges represent linear thickenings, evident both on the deep and superficial aspects of the epidermis. The dermis is molded into a negative counterpart of the epidermis, the dermal papillae coinciding with the superficial sulci.

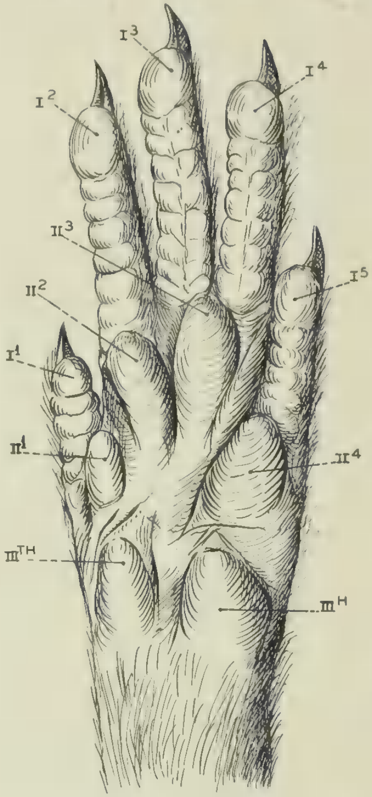

Fig. 7. Left manus of an insectivore (*Crocidura coerulea*), illustrating the generalized plan of volar pads. I^{1-5}, apical pads; II^{1-5}, interdigital pads; III^{TH}, thenar pad; III^{H}, hypothenar pad. Modified from Whipple.

MORPHOLOGICAL PLAN OF THE CONFIGURATIONS

It has been noted that the systems of ridges frequently form patterns. A *pattern* is an aggregation of ridges which are abruptly recurved, to com-

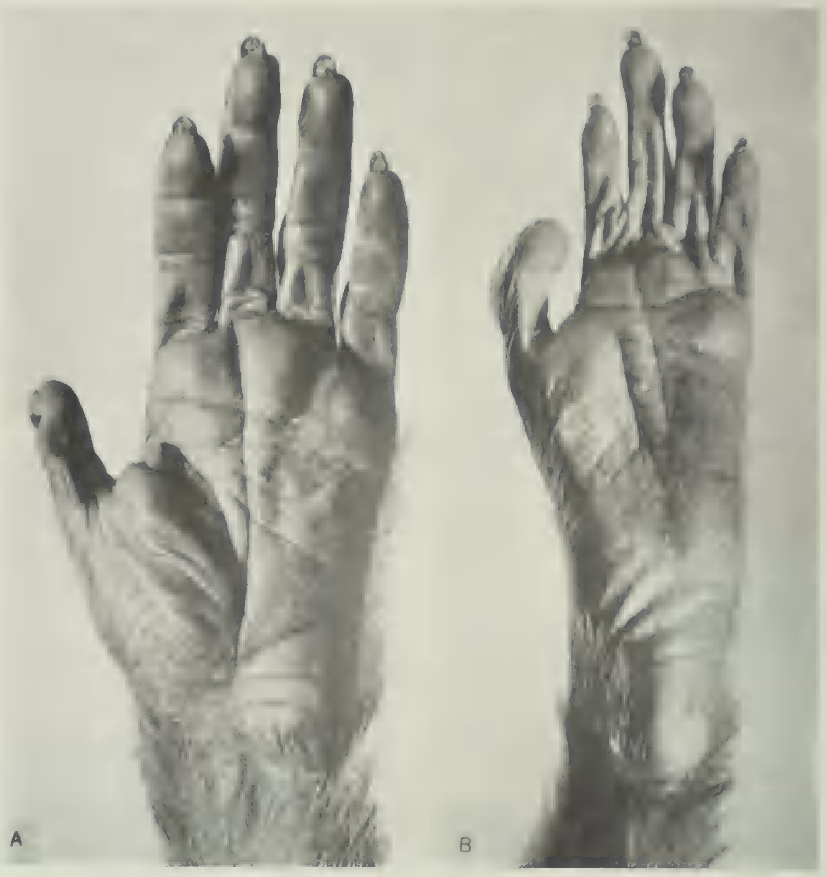

FIG. 8. Left manus (A) and pes (B), showing pads and the relation of the dermatoglyphics to the volar reliefs.

pose a concentric circular figure, a loop, spiral or other design. An *open field*, in contrast, is a monotonous succession of parallel ridges which are straight or only gently curved. The distribution of patterns and open fields is dependent upon the relief of the volar surface, and in considering the morphological plan of the configurations it is necessary to examine the character of the relief.

Of prime interest in this connection are the volar pads (walking pads; Tastballen). It is well to recall that in the generalized mammalian chiridium (fig. 7) there are eleven volar pads, grouped in three series. The most distal set comprises the *apical pads*, or balls of the digits. Next succeeding proximally there is a series of four *interdigital pads*, lying in the distal zone of the vola in relation to the interdigital intervals. Lastly, there are two pads, the *thenar* and *hypothenar*, in the proximal region of the vola.

Primates, in comparison with generalized walking forms, display a tendency for pads to undergo regression, a regression which is actually demonstrated in the embryonic history. The definitive pads of primates are less elevated and less precisely bounded at their bases, and may be diminished in expanse, suppressed entirely, divided or variously conjoined with neighboring pads. In both manus and pes of the rhesus monkey the apical pads are fairly distinct, as are the second, third and fourth interdigitals. But the remaining pads do not conform to the simple type shown in figure 7, and the situation is confused by the fullness of the thenar and hypothenar eminences, which are surmounted by the corresponding pads. Now, if the situations of the patterns of the manus (fig. 9A) be compared with the primitive pad arrangement (fig. 7) it will be evident that they conform in all respects excepting that there are two hypothenar patterns instead of the single one which would be expected in the light of the typical schema of pad arrangement. This character of the hypothenar configuration forms an example of pattern modification which is common throughout the primates, and is to be accounted for by reference to the state of the hypothenar pad. The hypothenar pad in *M. mulatta* is typically divided into proximal and distal elements, only the former being in most cases provided with a distinct summit bearing a pattern (fig. 8A). When the distal element is not markedly elevated its configuration is an open field. Some individuals, moreover, lack a thenar pattern (as in fig. 8A), the configuration of its site being then an open field. In the pes there is a like conformity of the pattern disposition to the topography of primitive pads, with a probable division of the hypothenar configuration comparable to that in the manus. Only rarely in the rhesus monkey does a true pattern occur in the proximal portion of the plantar hypothenar configuration.

In view of the correspondence of patterns and volar pads, the same morphological designations are applied to both. All patterns occupying pads of the series described above or their expected sites are termed *primary patterns*. Occasionally patterns occur elsewhere, as on the proximal and middle phalanges, or on the calcar region, occupying inconstant elevations which are not members of the primary series of pads. They are known as *secondary patterns*. Again, a pattern may be found lying in a depression rather than on a pad, as in the "hollow" of the palm. Such a configuration is distinguished as a *false pattern*.

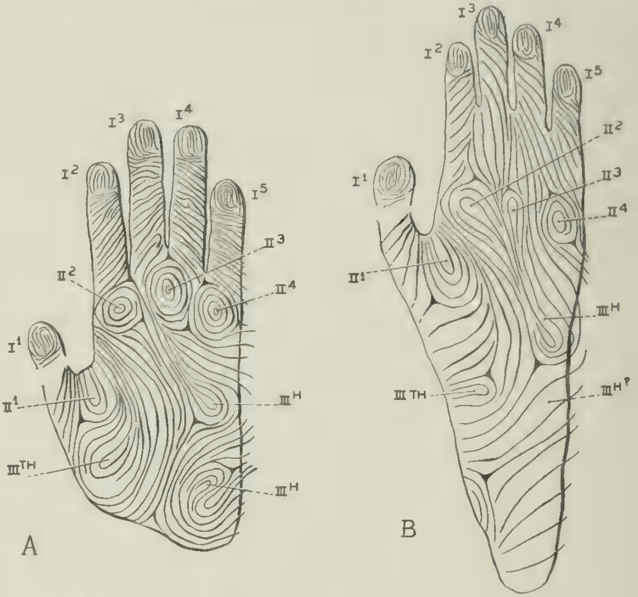

Fig. 9. Diagrams of left manus (A) and pes (B), illustrating the topography of dermatoglyphic systems. I^{1-5}, apical patterns; II^{1-4}, interdigital patterns; III^{TH}, thenar pattern; III^H, hypothenar patterns, distal and proximal. Individual variation is expressed in the suppression of some patterns and in unlike configuration of homologous areas.

The configurations of patterns, including all the ranks in the foregoing classification, are subject to wide variation. In what is generally assumed to be the most primitive type, the pattern is constructed in the form of a whorl (fig. 9A, II^{2-4}), a more or less circular series of concentric ridges. The design may be also any one of a variety of forms, as a loop (fig. 9A, II^1, $\mathrm{III}^{\mathrm{TH}}$), a double-loop figure (fig. 9A, $\mathrm{III}^{\mathrm{H}}$, proximal division) or a less readily definable deviation from the type of an open field (fig. 9, apical configurations). It must be emphasized, further, that corresponding patterns may be unlike in different individuals (compare fig. 9B, II^{2-4} with the corresponding configurations in fig. 8B), or unlike bilaterally in the single animal. A pattern may be even supplanted by an open field. It is thus apparent that individual and bilateral variation extends to major features of the configurations as well as to the less conspicuous ridge details.

In concluding the discussion of the plan of the dermatoglyphics it should be mentioned that triradii are disposed with a topographic regularity which admits the construction of a morphological schema supplementing that of the patterns (for details see Whipple, Schlaginhaufen).

FUNCTIONAL CONSIDERATIONS

The ridging of the volar skin enhances its contact properties in locomotion and prehension, reducing the tendency to slip in the manner of familiar devices such as the tread of a tire or the milling of a tool handle. Further adhesiveness is gained by the slight moistening of sweat, and the contact is rendered still more efficient by the yielding of the chiridial reliefs to pressure, the ridged surface being thus closely adapted to the conformation of objects. Th anti-slipping property of the specialized volar skin is recognized in the designations, "friction ridges" and "friction skin." It may be noted, in passing, that in certain New World monkeys (e.g., *Ateles*, *Lagothrix*) the ventral surface of the prehensile tail is similarly specialized.

Tactile sensitiveness may be mechanically enhanced by the presence of ridges, the drag to which they are subjected in passing over a surface being assumed to produce an agitation of the skin components which is more vigorous, and consequently more efficient in stimulating the contained sensory nerve-endings, than is the case in areas lacking ridges. The supposed importance of the tactile function is embodied in the following terms: Tastlinien (= epidermal ridges; friction ridges); Tastfiguren (= epidermal patterns; dermatoglyphic patterns); Tastballen, or Toruli tactiles (= volar pads; walking pads).

If ridged skin is to be credited with the functional attributes just mentioned, it may or may not follow that the particular arrangements of ridges are evolved in furtherance of these functions. According to one view the frictional quality is considered preeminent, and the various configurations, patterns and open fields, are regarded as adaptations toward the most efficient performance of that function, providing frictional resistance to counteract slipping in various directions. Another interpretation sees in the patterns an adaptation mainly concerned with the refinement of tactile discrimination. A third conception of the basis of configurational morphology, while granting both the functional attributes of ridged skin, is yet unwilling to accept either as the prime element in regulating the specific configurations. According to this last view it is considered that ridge direction, hence the production of particularized configurations, is dominated so completely by growth factors in embryonic development that ridge arrangements *per se* are devoid of independence. The ridge-forming capacity is regarded as the sole inherent quality of the volar skin, the whole organization of the dermatoglyphic territory, with its various patterns and open fields, being determined by growth phenomena having their main expression in the modeling of the volar reliefs. There is, then, no autonomy of a pattern, even though it be a member of the primary series; its appearance as a pattern is but a reflection of the complex growth forces producing the elevation on which it lies (or, in the instance of a false pattern, the depression). Variations in the form of an elevation are associated with variations in the configuration of the pattern, and the modeling of the elevation may be even such as to produce no pattern at all, but a simple open field.

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Chapter V

SKELETON AND JOINTS

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INTRODUCTION

Only a general description of the skeleton of *Macaca mulatta* is attempted here. It will require much research to work out the details of development, growth, structure and architecture of the bony framework of this animal. In the meantime the present description is offered. It should be stated, however, that this was prepared with the needs of experimental work in mind rather than the demands of descriptive anatomy.

The terms in general use in comparative anatomy and the usual classification of bones into long, flat and irregular, compact and cancellous, membrane and cartilage will be carried over from the standard human anatomies. In accordance with the main purpose of the chapter regional descriptions are followed; and in keeping with this plan the illustrations have been selected to show relationships, hence in only one or two cases are isolated bones pictured.

The drawings were made from an adult skeleton. Two roentgenograms of young skeletons are shown—these two being selected for specific purposes from the many that formed the basis of this study. It was found impracticable to publish more here, but the collection will be of use for detailed study in the future.

In the discussion of joints more emphasis is placed on movement than on structure. Only the more prominent ligaments are described. The range of movement was observed on animals under anesthesia, on those recently dead and on wet preparations from which the muscles had been removed, so that the ligaments were the only restraining factors.

In this connection the terms *diarthrosis* and *synarthrosis* are used to indicate the presence or absence of a joint cavity. The implication of presence or absence of movement in these terms is unfortunate, for one can readily recall diarthrodial joints in which movement is reduced to a minimum, and synarthrodial joints relatively free. The further classification of diarthroses on the basis of shape of articular surfaces is useful if correlated with degree of movement. But the correlation is not an absolute one.

Leaving out of consideration the joints that provide for growth or are present as phylogenetic holdovers, the most generally useful classification, when one is dealing with the living or properly preserved animal, would seem to be the one that expresses the number of movements possible, that is: uniaxial, biaxial and multiaxial.

In studying any prepared skeleton, itself a highly artificial thing, it is well to cultivate somewhat the attitude of mind of the paleontologist who attempts to reconstruct from his isolated fossil bones the entire animal complete even as to hair and facial expression. The student should visualize about the skeleton the investing periosteum, the contained marrow, the cartilage usually destroyed in the process of preparation, the continuity established by fibrous connective tissue, and finally the attached muscles. In short, the skeleton as it exists in the living body should always be the background.

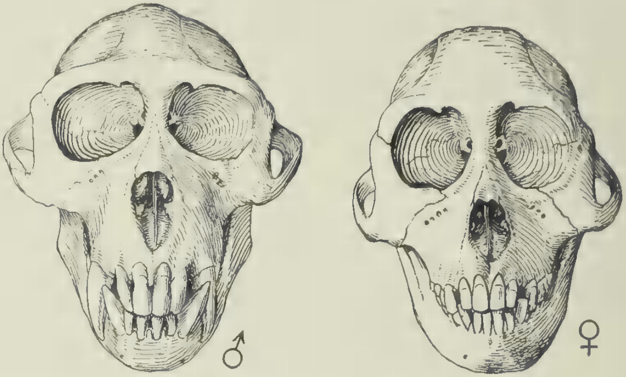

Fig. 10. Male and female skulls, seen from in front.

THE SKULL

(Figs. 10–16)

The shape and general proportions of the skull are adequately indicated by the illustrations and a craniometric study is beyond the scope of this work. Some attempt has been made to correlate the discussion with its various functions, but frequently convenience of description has interrupted the sequence. In any case one should think of the skull as a capsule for the brain, the eye, the ear, the olfactory organ, and in a less technical sense for the gustatory apparatus. The skeleton of the face has been profoundly modified by the masticatory apparatus, that of the cranium to a less degree. As in many animals, this mechanism is important in offense and defense. The skull also includes the upper part of the respiratory tract and the organs of voice.

With this general conception of the skull it appears that a description of the several regions and their interconnections will be the most satisfactory. The teeth, nasal cavity, hyoid bone, and larynx are discussed in other sections of this book (chapters II, VI, IX).

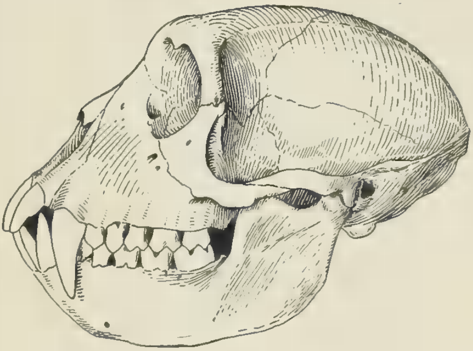

FIG. 11. The skull, seen from the side.

Anterior surface of the skull

(Figs. 10–12)

The skull as seen from the front is roughly pentagonal with the base in the supra-orbital region and the apex at the mandibular symphysis. Portions of the frontal, nasal, zygomatic, maxillary, premaxillary and mandibular bones are included. In addition parts of the lacrimal, ethmoid and sphenoid bones are described with the orbit.

This surface may be conveniently divided into a frontal area, an orbital region, an external nasal and an oral.

Frontal area. The frontal area is relatively flat and extends almost directly dorsally from the supra-orbital margin. It is formed entirely by the frontal bone. In the younger animals it is essentially unbroken; in the older there is an ovoid convexity on either side of a well marked midsagittal line. This elevation is due to an increase in the cancellous bone and no frontal sinus is present.

Orbital region (figs. 12, 13). The orbits are large, conical fossae separated by narrow cranial projections of the nasal cavities and a correspondingly narrow nasal projection of the anterior cranial fossa. The medial walls are essentially parallel to each other in the sagittal plane; the inferior are nearly horizontal; the superior and lateral are oblique. The four walls converge dorsally at the optic foramen, which is in line with the middle of the medial margin.

Margins of the orbit (fig. 13). The orbital margin on either side is formed by the frontal, maxillary and zygomatic bones. The frontal forms all of the superior margin and a little less than half of the medial and lateral. The maxillary bone completes the medial margin and forms the medial half of the inferior margin. The zygomatic bone completes the inferior and lateral margins. Structures associated with the orbital margin are the supra-orbital notch, the zygomaticotemporal, the zygomaticofacial and infra-orbital foramina, and the fossa for the lacrimal sac.

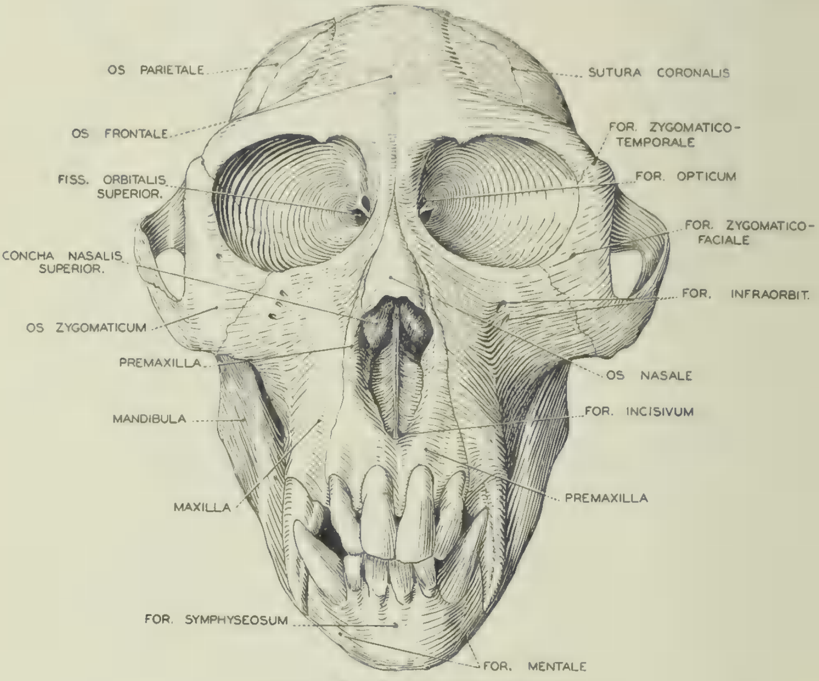

FIG. 12. The skull, norma frontalis.

Near its medial end the superior margin is broken by a large *supra-*

orbital notch (incisura supra-orbitalis), which is bounded laterally by a distinct spine. The other margins are unbroken except as they are crossed by the suture lines. A short distance (2 or 3 mm.) from the lateral margin in the frontozygomatic suture is the *zygomaticotemporal foramen*, which leads through a small canal into the orbit. Entirely within the zygomatic bone near the junction of the lateral and inferior segments of the orbital margin is the *zygomaticofacial foramen*. This varies from a relatively large opening to an extremely minute one. Below the middle of the inferior margin are from two to four or more *infra-orbital foramina*. They are entirely within the maxillary bone and are continued dorsally as short canals that perforate the floor of the orbit. Just behind the inferior half of the medial margin is the *fossa for the lacrimal sac*. It is almost entirely on the lacrimal bone. This is of course the anterior part of the medial wall of the orbit.

Foramina and fissures of the orbit (fig. 13). Within the orbit are the fossa for the lacrimal sac, just described, the optic foramen, the superior and inferior orbital fissures, the zygomatico-orbital and infra-orbital foramina.

Either the *optic foramen* or the *superior orbital fissure* might be taken as the apex of the orbit. The foramen is a little superior and medial to the fissure. Both structures are in the sphenoid bone and both connect the orbit with the middle cranial fossa. Along the inferior wall of the orbit in its dorsal part is the *inferior orbital fissure*. This connects the orbit with the infratemporal and pterygopalatine fossae. The fissure is bounded by the greater wing of the sphenoid, the zygomatic and maxillary bones. It appears bifid at its ventral end, but the medial branch is the *infra-orbital sulcus* of the maxillary bone. There is a small foramen, the *zygomatico-orbital*, on the lateral wall in the frontosphenoidal suture. On the medial wall there are one or more small openings suggestive of the *ethmoidal foramina*, but lying well above the fronto-ethmoidal suture.

External nasal aperture (fig. 12). The nasal opening is pyriform, with its base above. The base is formed by the fused nasal bones. The premaxillary bones forming the lateral margins converge to meet at the alveolar processes. Through the external aperture one may identify the *conchae* on the lateral nasal walls and the *septum* in the midsagittal line. The nasal cavity is described more fully in chapter IX.

Oral region (figs. 11, 12). This region is narrow when viewed from the front. The incisor and canine teeth are readily examined but the others present only their buccal surfaces. Their occlusion is better discussed with the lateral surface. The upper incisors are in the premaxillary bones. The mandible, which recedes rapidly from the alveolar margin to the plane of the first molar, has several small foramina on this surface. There is an unpaired foramen in the midline (*foramen symphyseosum*) which is one end of a sagittal canal that completely perforates the mandibular symphysis. There are one or two foramina (*foramina mentalia*) on either side near the inferior margin. In one specimen at hand there is, on the left side, one in the plane of the second premolar and one in line with the first molar; on the right side, two in the plane between the second premolar and the first molar and one between the first and second molars. The larger and usually the more anterior of these communicates with the mandibular canal.

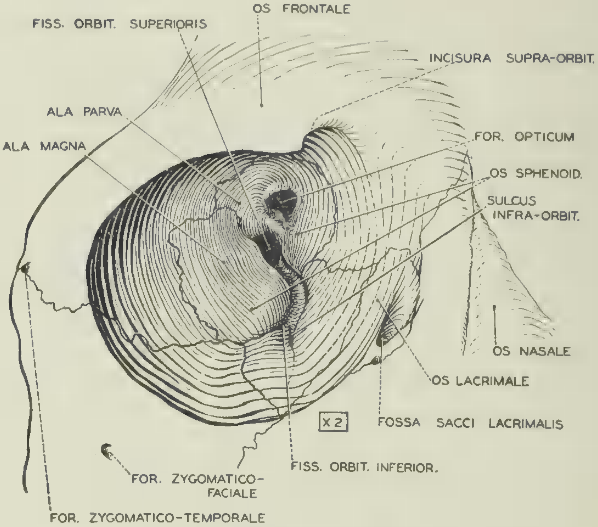

FIG. 13. The right orbit.

Lateral Surface of the Skull

(Figs. 11, 14)

Here one has another view of many of the structures already described. The bones forming this surface are the frontal, parietal, nasal, zygomatic, temporal, maxillary, sphenoid and mandibular. Just a small section of the palatine appears between the maxilla and the lateral pterygoid plate.

It is convenient to discuss this area in terms of a temporal fossa, an infratemporal fossa, a pterygopalatine fossa and a temporomandibular region. The last includes the joint.

Temporal fossa (fig. 11). The temporal fossa, which includes most of the lateral surface of the skull above the zygomatic arch, is relatively featureless. The inferior boundary is the zygomatic arch laterally and the infratemporal crest medially. The anterior boundary includes the frontal process of the zygomatic bone and the zygomatic process of the frontal. In the suture between the two processes is the *zygomaticotemporal* foramen. This is continued through a canal into the orbit. The superior limit is the *temporal line*, which is well defined in its anterior part where it begins as a crest on the frontal and zygomatic bones but is otherwise indistinct in the younger specimens. The position of the line varies. In the younger specimens it is near the parietosquamosal suture; in the older it approaches the sagittal.

Infratemporal fossa. This is the space between the mandible laterally, the lateral pterygoid plate medially and the maxilla anteromedially. The horizontal portions of the squama of the temporal (squama temporalis) and the great wing (ala magna) of the sphenoid form an incomplete superior wall. While the junction of the temporal and infratemporal fossae is indicated by a well marked *infratemporal crest* the two communicate with each other freely. The sphenoidal portion of the crest bears a spine.

The openings of interest in the infratemporal fossa are the inferior orbital and pterygomaxillary fissures, the oval and mandibular foramina. Between the maxillary bone and the great wing of the sphenoid there is a narrow *inferior orbital fissure* which connects the fossa with the orbit. On the medial wall of the fossa there is a small vertical slit, the *pterygomaxillary fissure*, leading into the pterygopalatine fossa. The name describes its boundaries. On the lateral surface of the lateral pterygoid plate near its base is an elliptical opening which connects with the middle cranial fossa at the *foramen ovale.* The ramus of the mandible which forms the lateral wall of the fossa has the *mandibular foramen* about the middle of its medial surface. Further discussion of the mandible is given in a later section.

Pterygopalatine fossa (fig. 15). This is a very small space in the rhesus monkey. The ventral boundary is the maxilla, the dorsal is the pterygoid process of the sphenoid, and the medial is the vertical plate of the palatine bone. The connections appear the same as in man. The fossa is continued orally to open on the palate at the *greater palatine foramen.* On its medial wall is the *sphenopalatine foramen* through which it communicates with the nasal cavity. Laterally it is connected with the infratemporal fossa through the pterygomaxillary fissure. Its continuity with the orbit is through the inferior orbital fissure. On the dorsal wall of the fossa are found the *foramen rotundum* (fig. 16) and the ventral opening of the *pterygoid canal.* The former connects it with the middle cranial fossa. The canal passes through the sphenoid in the sagittal plane to have its posterior opening at the petrosphenoidal synchondrosis.

Temporomandibular region (figs. 11, 14). Under this general term are included the zygomatic arch, the temporomandibular joint, the external auditory meatus, and a few of the neighboring structures.

The *zygomatic arch* is formed in the usual way by the temporal process of the zygomatic bone and the zygomatic process of the temporal. The superior margin and the lateral surface of the latter are continued dorsally as a crest above the external acoustic meatus. The inferior margin as it passes dorsally is interrupted at the articular tubercle. There is here on the inferior surface of the temporal bone in linear succession from ventral to dorsal the articular tubercle, the mandibular fossa, the postarticular (postglenoid) process and the external auditory meatus (meatus acusticus externus). The *articular tubercle*, in part continuous with the inferior margin of the zygomatic process, is convex and large. Dorsal to it lies the *mandibular fossa*, which is rather deep. Immediately dorsal to the lateral part of the fossa is a long, strong spine, the *postarticular* process. Directly medial to this is the *petrotympanic fissure*, which forms the posterior limit of the mandibular fossa in its medial part. A small foramen is

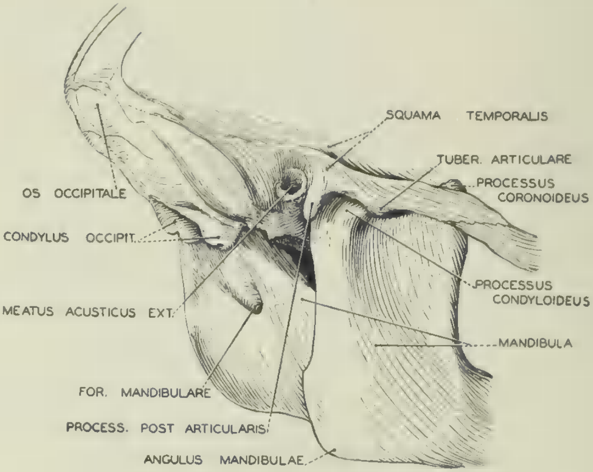

Fig. 14. The right temporomandibular region.

frequently seen at the lateral end of the fissure. The tympanic bone surrounds the external acoustic meatus except in its superior part, where it is largely replaced by the squamous. Just dorsal to the external acoustic meatus is a distinct crest which curves upwards and backwards to be continuous with the external occipital crest.

Temporomandibular joint (figs. 11, 14). This diarthrosis is between the mandibular condyle, on the one hand, and the mandibular fossa and articular tubercle of the temporal bone on the other. The movements present are depression and elevation, protraction and retraction and a lateral movement (rotation) to either side.

The entire joint is enclosed in a capsule which is thickened laterally as a *temporomandibular ligament.* This ligament is nearly vertical when the mandible is elevated and retracted but runs downward and forward when the mandible is protracted. It seems to tighten only in protraction.

When the capsule is opened a complete articular disc is seen. Now it appears that the articular surface on the temporal bone is large and includes the entire tubercle, an area medial to the latter, and the mandibular fossa dorsal to the tubercle. In all there is at least twice as much articular surface on the temporal bone as on the mandible.

Inferior surface of the skull

(Fig. 15)

With the mandible removed the inferior surface may be conveniently discussed in terms of palatine, pharyngeal and occipital regions. Of course the infratemporal and temporomandibular areas are in view.

Palatine region (fig. 15). The hard palate is formed by the premaxillary, maxillary and palatine bones. The boundaries, except dorsally, are the alveolar processes with the teeth. There are eight permanent teeth on each side in all fully mature catarrhine monkeys. In the young specimens the width of the palate is rather more than half its length, in the older slightly less than half. The structures of most interest are the sutures, the incisive foramina, and the posterior palatine foramina.

The *maxillopremaxillary suture* was present in all of the skulls examined. Its lateral end is between the second incisor and the canine. A *median palatine suture* separates the bones of the two sides. At the anterior end of this suture lie the large *incisive foramina.* It perhaps should be pointed out that these foramina not only perforate the bone but also the mucosa and so connect the oral and nasal cavities in the living animals. It is rather hard to decide whether the thin plate of bone separating the incisive foramina belongs to the premaxilla or vomer. The author is rather inclined to assign it to the premaxilla. The maxillary and the palatine bones are separated by a suture, the *transverse palatine*, which is transverse in its medial part but sagittal in its lateral. At the junction of its two segments and just medial to the last molar is the *posterior* or *greater palatine foramen* (foramen palatinum majus). This is continued upward as a canal into the pterygopalatine fossa.

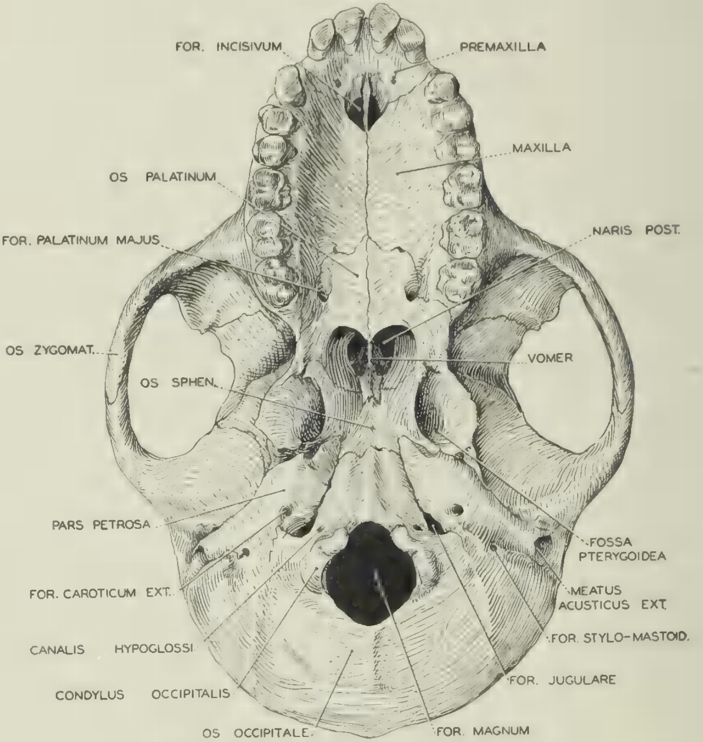

Fig. 15. The skull, basis cranii externa.

Pharyngeal region (fig. 15). In the pharyngeal region are the posterior nares, the pterygoid processes, the auditory tubes and the oval foramina. The temporal and sphenoidal bones are in such close contact that no foramen lacerum is present.

The *posterior naris* is subtriangular with its base on the hard palate. The inferior boundary is the horizontal plate of the palatine bone, the lateral boundary is the vertical portion of the same bone, and the medial wall is the vomer. Where the horizontal plates of the two palatines meet there is a varying posterior nasal spine. In some specimens there is a free dorsal tip; in others the margin curves upward at this point and blends with the nasal septum.

The *pterygoid process* of the sphenoid on either side is made up of a small medial and a large lateral plate. Between the two plates is the *pterygoid fossa.* The *medial pterygoid plate* is relatively small and forms a septum between the nasopharynx and the pterygoid fossa. Inferiorly it ends in a spine, the *hamulus*, directed dorsally. The *lateral pterygoid plate* is four or five times as wide as the medial and forms a partition between the pharyngeal region and the infratemporal fossa. The posterior part of its base is perforated by one or two foramina which bring the foramen ovale into communication with the infratemporal fossa. The *foramen ovale* lies medial to the dorsal end of the lateral pterygoid plate between the great wing of the sphenoid and the petrosal part of the temporal. For the most part it is bounded by the sphenoid. Through one or more openings which pierce the base of the lateral pterygoid plate it communicates with the infratemporal fossa. The *pharyngeal orifice of the auditory tube* is just dorsal to the foramen ovale. It runs laterally and slightly dorsally to reach the tympanic cavity. Its course is essentially parallel to that of the petrotympanic fissure.

Occipital region (fig. 15). This term is used to designate the structures near the foramen magnum and would include the foramen itself, the occipital condyles, the hypoglossal canals, the jugular foramina, the external orifices of the carotid canals, and the equivalent of the stylomastoid foramina.

The *foramen magnum* is roughly hexagonal. Its anterior boundary is the basilar portion of the occipital. In the younger skulls the basioccipital has fused with neither the exoccipital nor the basisphenoid. In most of the specimens examined, however, it had fused with the former but not with the latter. The paired *occipital condyles* are placed obliquely lateral to the anterior half of the foramen magnum. The length of the condyles is three or four times their width. They are irregularly convex and usually show a notch along the medial margin.

The *hypoglossal canal*, short and cylindrical, is superior to the condyle, just a little anterior to its middle. Lateral to the dorsal end of the occipital condyle is the *jugular process*, immediately anterior to which is the *jugular foramen.* This foramen, which is rather large and somewhat elliptical, is formed in part by the occipital bone and in part by the temporal.

The external orifice of the carotid canal (*foramen caroticum externum*), which is entirely within the petrous portion of the temporal bone, is either directly anterior or anterolateral to the jugular foramen. From this opening the canal runs at first superiorly and laterally, then medially and anteriorly in a gentle curve to reach the apex of the bone and end in the middle cranial fossa.

The *inferior orifice of the facial canal* (stylomastoid foramen) lies immediately dorsal to the external acoustic meatus about a centimeter in from the lateral surface of the skull.

A transverse line passing just behind the external acoustic meatus will intersect the stylomastoid foramen, the jugular foramen, the hypoglossal canal, and the anterior part of the foramen magnum. A similar line just in front of the meatus will pass through the external opening of the carotid canal.

At the extreme dorsal margin of the basis cranii externa is the *external occipital protuberance* (*inion*). From this the *superior nuchal lines* pass laterally to the junction of the occipital, parietal and temporal bones, where they are continued as two diverging crests. The more direct continuation follows the parietotemporal suture, then along the temporal to end behind the external acoustic meatus. The other limb, less marked, follows the temporo-occipital suture. A median crest joins the external occipital protuberance with the posterior margin of the foramen magnum.

Internal surface of the base of the cranium

(Fig. 16)

This region is naturally divided into anterior, middle and posterior cranial fossae. Many of the structures seen here have already been described.

Anterior cranial fossa (fig. 16). The anterior fossa is formed by parts of the frontal, ethmoid and sphenoid bones. For the most part it presents two large convex areas, the superior walls of the orbits, separated by a median concave area. In the middle in the anterior part of the fossa is the *cribiform plate* (lamina cribrosa) of the ethmoid. The plate is elliptical in outline, relatively small and entirely surrounded by the frontal bone. It is very thin and is frequently broken in cleaning the skull. Through its foramina the anterior cranial fossa communicates with the nasal cavity. Dorsal to the cribriform plate in the midline there is a suture between the two halves of the frontal. At the posterolateral angle of the fossa are one or more small foramina that open on the lateral wall of the orbit. In the cranial cavity these foramina are in continuity with the *meningeal sulci*. One of these at least is worthy of comment. Beginning at the foramina just mentioned it crosses the squama temporalis in a general way parallel to the squamosal suture to reach the squamopetrosal suture. At its junction with the latter is a foramen which reaches the outer surface of the skull at the lateral end of the petrotympanic fissure. These foramina at either end of the sulcus may be called the anterior and posterior meningeal.

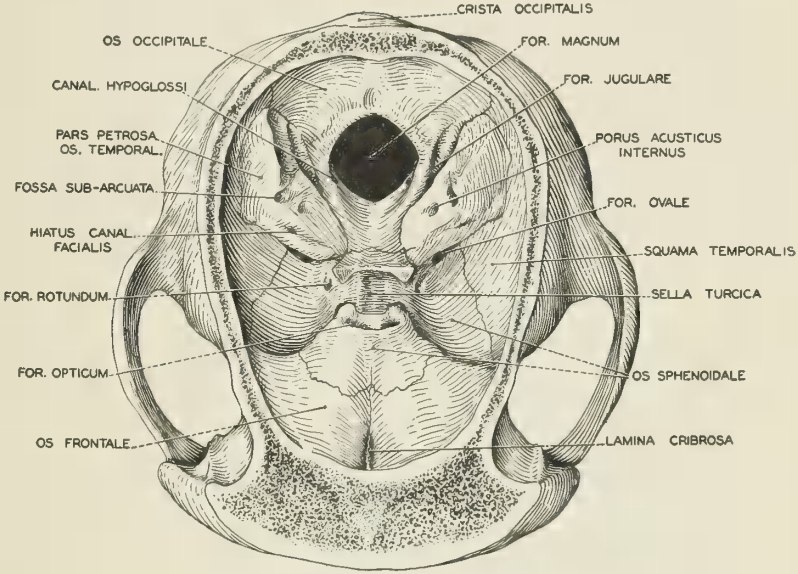

FIG. 16. The skull, basis cranii interna.

Middle cranial fossa (fig. 16). The middle cranial fossa presents many structures of interest, including as it does the optic foramina, the sella turcica, the clinoid processes, the superior orbital fissures, the round foramina, the oval foramina, the internal openings of the carotid canals, the carotid sulci, the meningeal sulci, the hiatuses of the facial canal, and the petrosquamosal sutures.

The fossa, which includes portions of the temporal and sphenoid bones, may be divided into a small central area and large right and left lateral.

The central area is quadrilateral and includes the optic foramina and the hypophyseal fossa. The *optic foramina*, large and circular, lie in the anterior part of the fossa, one on either side of the midline. They are separated from each other by a heavy vertical column of bone. These foramina together with the superior orbital fissures, and small intermediate foramina, the *paroptic*, connect the cranial cavity with the orbits. The *hypophyseal fossa* marked at each of its four corners by a *clinoid process* occupies the dorsal part of this area. It dorsal wall is the *dorsum sellae*. The *anterior clinoid* processes are dorsal to the lateral part of the *optic foramina*. The *posterior clinoid processes* are the free angles of the dorsum sellae. In all of the specimens examined there was a synchondrosis between the basisphenoid and the presphenoid.

In the lateral segment of the middle cranial fossa on either side immediately inferior to the optic foramen and separated from it by the anterior clinoid process is the *superior orbital fissure*. Dorsal to the lateral part of the superior orbital fissure is the *foramen rotundum*, which connects the cranial cavity with the pterygopalatine fossa. It is more in the nature of a canal than a foramen. Dorsal to the foramen rotundum and at the apex of the petrous portion of the temporal bone is the internal orifice of the *carotid canal*. The *foramen ovale* is between the dorsal border of the great wing of the sphenoid and the petrous portion of the temporal, though largely surrounded by the former. It is dorsolateral to the foramen rotundum and directly connects the cranial cavity with the pharyngeal region and by the foramina perforating the lateral pterygoid plate with the infratemporal fossa. The hiatus of the *facial canal* is large and easily identified about the middle of the anterior surface of the petrous portion of the temporal. On the cranial surface there is a distinct *petrosquamosal suture*.

Posterior cranial fossa (fig. 16). The posterior fossa is made up largely of the occipital bone, the posterior surface of the petrosal and the dorsum sellae of the sphenoid. The structures of interest are the foramen magnum, the hypoglossal canal, the jugular foramen, the internal acoustic meatus, the arcuate eminence, the subarcuate fossa, and several fossae on the squama occipitalis.

The *foramen magnum* has been described with the basis cranii externa and needs no further discussion. Lateral and superior to the anterior part of the foramen magnum is the internal opening of the *hypoglossal canal*. This is occasionally double. Both of the structures just described are entirely within the occipital bone. Lateral to the hypoglossal canal between the occipital and temporal bones is the *jugular foramen*. Posterolaterally this foramen is continuous with the sigmoid portion of the *transverse sulcus*, anteromedially with a *petro-occipital sulcus* (inferior petrosal).

The dorsal surface of the petrous portion of the temporal bone presents two large orifices, a more medial into the *internal acoustic meatus* (porus acusticus internus), a more lateral into the *subarcuate fossa*. A further examination of the internal acoustic meatus shows four secondary openings at its lateral end. The confluence of the transverse and sagittal sulci is at about the middle of the cranial surface of the squama occipitalis and on the external surface would be marked by a point somewhat below the external occipital protuberance.

VERTEBRAL COLUMN

(Figs. 22, 41)

The vertebral column normally consists of a cervical region of seven vertebrae, a thoracic region of twelve, a lumbar region of seven, a sacral region of three, a caudal region of about twenty, and the intervening intervertebral discs.[1] In the living animal the cervical region is usually dorsiflexed, the thoracic and lumbar ventroflexed, the sacral and caudal slightly dorsiflexed.

The unmodified vertebrae have as in man a ventral body and a dorsal arch surrounding the vertebral foramen. From the arch are the transverse processes directed laterally, the spinous processes dorsally, the superior articular processes cranially and the inferior articular processes caudally.

Cervical vertebrae

These are characterized by relatively small bodies and relatively large arches. The cephalic surface of each body is concave, the other surfaces essentially plane. The *vertebral foramina* are large and pentagonal. The base of each *transverse process* is perforated by the *foramen transversarium*. The transverse processes of the fourth, fifth and sixth vertebrae end in conspicuous dorsal and ventral tubercles. The ventral tubercle of the sixth is especially large and laminiform. The spinous processes are rather short but increase in length from the third to the seventh. The latter, however, is considerably shorter than that of the first thoracic. The articular surfaces of the articular processes are flat and make contact with those of the adjacent vertebrae in an oblique plane between the frontal and horizontal.

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[1] According to the data collected by Sherrington (1892) and Schultz (1930), based on 89 specimens of the rhesus monkey, the thoracic vertebrae numbered 12 in 97 per cent (86 specimens), 13 in 3 per cent (3 specimens), while the lumbar vertebrae numbered 7 in 94 per cent (84 specimens), 6 in 6 per cent (5 specimens); in 91 specimens the combined thoracic and lumbar column was even more stable, for the thoracolumbar vertebrae numbered 19 in 98 per cent (89 specimens), 18 in 2 per cent (2 specimens). According to Schultz, there were 3 sacral vertebrae in each of 16 specimens.

Atlas and epistropheus

The first and second cervical vertebrae require special descriptions. The *atlas* consists of a long dorsal arch, a short ventral arch and the paired lateral masses. The ventral arch dorsally has an articular surface for the dens of the epistropheus, and ventrocaudally a long keel-like spine for the cephalic attachment of the prevertebral muscles. The lateral masses are made up of the articular and transverse processes. The superior or occipital articular surface is long, concave, and faces medially and cephalically. The inferior or epistropheal surface is much smaller, oval and but slightly concave. The transverse process is small and has its base perforated by the foramen transversarium. This foramen is continuous dorsally with a sulcus which in turn ends in a foramen medial to the dorsal end of the superior articular process.

The *epistropheus* or axis consists of a body, dens, arch and several processes. The caudal face of the body is slightly concave, the cephalic carries the dens. The vertebral foramen is almost circular. The transverse processes are small, the spinous large. The superior articular processes are slightly convex and in an oblique plane between the horizontal and the sagittal; the inferior are flat and are in a plane between the frontal and horizontal.

Thoracic vertebrae

The thoracic vertebrae increase in size from the first to the twelfth. The bodies form about a half of an ellipse. Near the junction of the lateral and dorsal surfaces are the articular facets for the heads of the ribs. These are rather small and not readily identified on a disarticulated column. From a specimen at hand it seems that the upper eight (or seven) articulate with two ribs, the lower four (or five) with but one. The vertebral foramina are subcircular. The transverse processes are relatively large and from the first to the tenth have articular facets for the tubercles of the ribs. The spinous processes are long and are directed dorsally and caudally from the first to the ninth, the tenth is transitional (anticlinal), the eleventh and twelfth are distinctly lumbar in character. The articular processes are flat and meet in an oblique plane which approaches the horizontal. The eleventh and twelfth thoracic vertebrae and the first, second and third lumbar have distinct *accessory processes* (anapophyses) just ventral to the caudal articular process.

Lumbar vertebrae

(Fig. 22)

The seven lumbar vertebrae continue the series gradually increasing in size. The bodies are large and essentially reniform. The arch with the processes is suggestive of strength. The vertebral foramina decrease in size. The transverse processes increase in size from the first to the seventh. On the first they are rather small. In general they are directed laterally and cephalically but the last two end in spines directed cephalically. The spinous processes are heavy with a slight cephalic inclination. The articular processes have their articular surfaces opposing each other in an oblique plane tending toward the sagittal.

Sacrum

(Fig. 22)

The sacrum represents the fusion of three vertebrae. The fusion apparently occurs laterally before it does centrally although in one specimen at least the articular processes between the first and second vertebrae are the last elements to fuse. This suggests that the sequence is first the transverse and costal elements, then the bodies, and finally the articular processes. It will be perhaps most convenient to describe the bone in terms of its surfaces. The pelvic surface is essentially smooth, being interrupted only by the two pairs of *anterior sacral foramina* and the transverse lines. The appearance of the latter varies with the age of the animal. The cephalic surface presents the centrum, the superior aperture of the sacral canal, the superior articular processes and the cephalic margin of the alae. The dorsal and lateral surfaces may be described as one. In the midline is the *medial sacral crest* formed by the spinous processes. The first spine is very large, the second and third rather small. On either side of the midline is the *sacral articular crest* formed by the articular processes. The superior process of the first and the inferior process of the third are essentially unmodified. The others form diarthrodia' joints in the young but are fused in the adult. There are two pairs of *posterior sacral foramina*. Lateral to the foramina is the *crest of the transverse processes*. In the region of the first two vertebrae the sacrum is greatly expanded laterally, forming the large wings. The cephalic two-thirds of each ala is rough, while the caudal third is occupied by the *iliac articular surface*. This is reniform, with its long axis essentially transverse. The caudal surface of the sacrum is formed by the centrum, the inferior aperture of the sacral canal, the inferior articular and the transverse processes.

Caudal vertebrae

(FIG. 22)

These become increasingly small and modified and there would seem to be no point in discussing them in detail. There is a vertebral foramen in the upper four, a rudimentary spine on the first and second, transverse processes on the first six, articular processes on the first five. The junction of the fourth and fifth is the plane of the ischial tuberosities. Prominent *chevron bones* are present on the ventral surfaces of the more proximal members of this series.

Joints of the vertebral column

The bodies of the successive vertebrae are connected by the intervertebral discs, the arches by the diarthrodial joints between the articular processes. The intervertebral disc contains a large *nucleus pulposus.* I have not examined the cervical region for diarthroses between the lateral parts of the bodies. The only vertebral ligaments examined in any detail are the intervertebral and those in the atlanto-epistropheo-occipital region.

The *interspinous ligament* is formed of elastic tissue and is thick and deep. The interspinous spaces are about equal to the spines and they are filled by the ligaments which pass without interruption onto the laminae. The *anterior longitudinal ligament* is well developed, especially in the lumbar region. The *intertransverse ligaments* are flat and thin. There is a *supraspinous* and a *posterior longitudinal ligament.*

When the muscles are removed from the back of the neck there appears a strong dorsal *atlanto-epistropheal membrane.* In the same plane is a heavy fascial layer between the atlas and the occipital bone. This latter is superficial to the m. rectus capitis posterior minor. Beneath the muscle is the *posterior atlanto-occipital membrane.* On opening the vertebral canal and examining the region of the dens several ligaments are seen. First the posterior longitudinal ligament bifurcates and attaches to the occipital bone on either side of the foramen magnum. This perhaps should be designated as the lateral part of the *tectorial membrane.* Running transversely are two fibrous bands. The narrower, more caudal is the *transverse ligament* of the atlas; the wider, more cephalic is the *alar.* The interspace between the tip of the dens, the alar ligament and the occipital bone is filled by fibrous bands running both obliquely and longitudinally.

Movements of the vertebral column. The data given on the atlanto-occipital and atlanto-epistropheal joints are from a dissected specimen, for in the living it did not seem possible to separate these joints from their neighbors. For the remainder of the column observations were made on an animal in deep anaesthesia and on one recently dead.

Dorsal flexion is the freest movement at the *atlanto-occipital* joint. The others are rather limited.

Rotation is free at the *atlanto-epistropheal* joint, as in dorsal flexion. The latter is more than the arrangement of the ligaments would suggest. During rotation there is a little oblique displacement.

For the cervical region as a whole, including the joints just described, dorsal flexion permits the back of the head to be brought into contact with the vertebral spines. Ventral flexion is slightly less free, and the mandible does not quite touch the sternum. Lateral flexion permits the side of the head to be brought into contact with the upper surface of the shoulder. Rotation and torsion combined permit a movement of from 90° to 130°. The latter is perhaps nearer the true figure as it was obtained from an animal under anesthesia.

In the thoracic region flexion, extension and the lateral movements are free but not of great range. Torsion is present but limited.

In the lumbar segments flexion and extension are present but limited and are exceeded by the lateral movements. Torsion is practically absent.

The caudal region can be flexed in any direction.

THORAX

(Figs. 18, 41)

The thorax consists of the thoracic vertebrae, the ribs with their cartilages, and the sternum. In its general shape it is perhaps intermediate between the human and the quadruped. The superior aperture is sub-elliptical in outline with the transverse diameter exceeding the antero-posterior. With the clavicles in position this aperture is essentially triangular. The inferior aperture is roughly circular. As a whole the thorax approaches the form of a truncated cone or pyramid.

The thoracic vertebrae have been discussed in the description of the vertebral column.

Ribs

(Fig. 41)

The ribs, *costae*, usually number twelve pairs. Of these eight are vertebrosternal, two are vertebrochondral, and two are vertebral. The upper ten are each made up of a head which articulates with the vertebral bodies, a tubercle which articulates with the vertebral transverse process, a neck intermediate between the head and tubercle, and a body extending from the tubercle to the costal cartilage. The eleventh and twelfth ribs usually have no tubercles. A subcostal sulcus is seen on the inner surface of the caudal margin of the second to the tenth ribs.

The ribs increase in length from the first to the seventh, the costal cartilages from the first to the ninth.

The costal cartilages show various degrees of ossification. As seen in the roentgenogram (fig. 17) it is essentially linear. It would appear to be central, rather than peripheral, but this has not been checked by section.

Sternum

(Fig. 17)

The sternum consists of seven bony segments joined by cartilage and terminating caudally in a segment of cartilage.

The most cranial bony segment, the *manubrium*, is the largest. It has the outline of an octagon. The other bony segments are nearly rectangular. They increase in length from the second to the fourth, then decrease to the sixth. The seventh, the *xiphoid*, is longer and narrower than any of the preceding. The intersegmental cartilages decrease in length from the first to the fifth and each articulates with a costal cartilage on either side. The sixth is longer and articulates with two costal cartilages, those of the seventh and eighth ribs.

Joints of the thorax

The joints of the thorax may be grouped as costovertebral, chondrosternal, intrasternal and interchondral.

Costovertebral articulations. These joints are between the heads and tubercles of the ribs on the one hand and the bodies and transverse processes of the vertebrae and the intervertebral discs on the other. In general it may be said that the head of the rib articulates about equally with the body of its corresponding vertebra, the body of the vertebra above and the disc between the two vertebrae. The tubercle of the rib articulates with the transverse process of its corresponding vertebra.

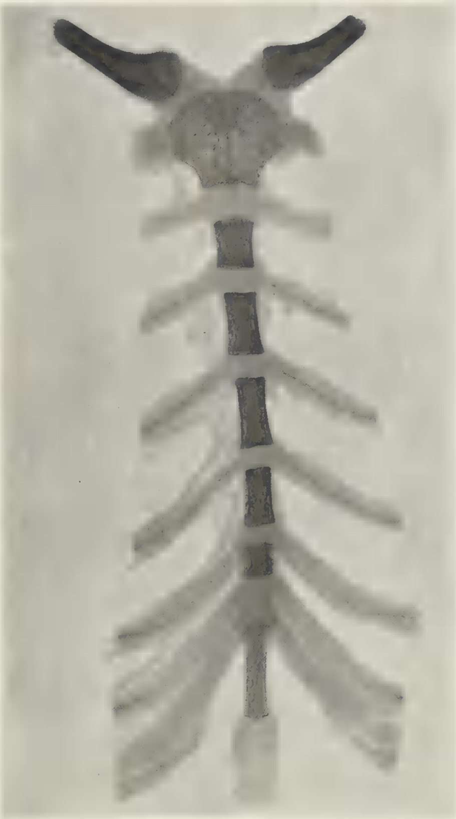

Fig. 17. The sternum; roentgenogram of young animal. The partial ossification of the costal cartilages is clearly seen.

For the most part it is a repetition of the story in man. As a matter of detail in a specimen at hand the first rib articulates with the first thoracic vertebra and the disc cephalic to it, the second to the eighth follow the general description, although the rib is moving more and more toward its own vertebra. The ninth and tenth join their own vertebrae and the disc above, the eleventh is largely on its own vertebra but touches the disc. The twelfth is entirely on the twelfth vertebra but near its cephalic margin. The joint between the tubercles and the transverse processes are present for the upper ten ribs and may occur for the eleventh. In a specimen at hand it is present on the left side but not on the right.

Movements of the ribs. The ribs for the most part are placed so that they present an inner and an outer surface and a cephalic and caudal margin. The vertebral end of the inner surface faces ventrally, the rest of it mediocaudally. The outer surface is naturally the opposite. The first rib has cephalic and caudal surfaces and inner and outer margins. The second, third and fourth are intermediate to the descriptions just given: The second tends to be more like the first, while the fourth approaches the general condition.

The principal movement is a rotation at the costovertebral joints. The axis is through the neck of the rib. The general result of this movement is an increase in the dorsoventral and transverse diameters of the thorax accompanied by a displacement of the sternum cephalically and ventrally. Without going into great detail it may be pointed out that in the case of the first rib the outer margin is raised slightly, the sternal end is carried cranially and there is a torsion of the costal cartilage. For the other sternal ribs there is a tendency for the outer surface to face more cranially. This is accompanied by a torsion of the cartilages and a movement at the chondrosternal joints in some instances about a dorsoventral axis, in some around an oblique modification of this. The twelfth and usually the eleventh ribs are free to move in any plane.

STERNOCLAVICULAR REGION

This includes the manubrium sterni, the first costal cartilage already described with the thorax, the medial end of the clavicle and the sternoclavicular joint. The latter alone needs a detailed description.

Sternoclavicular joint. This is a diarthrosis with an articular disc. On the clavicle the articular cartilage covers the ventral surface of the medial end; on the sternum it covers a part of the dorsal surface adjacent to the cephalic angle. A small area on the cephalic surface of the first costal cartilage is also articular. Dorsal to the sternum the joints of the right and left sides are separated by a distance of less than a millimeter. In the specimens examined the sternal articular surface was convex, with the long axis transverse; the clavicular was also convex, but with its long axis nearly cephalocaudal. This would suggest that elevation and depression occurred between the disc and the sternum, protraction and retraction between the disc and the clavicle. Only three specimens were used and this may not be the usual picture.

The capsule is rather strong but long and loose and the clavicle and sternum are readily separable. There is an interclavicular ligament across the jugular notch. The weakest segment of the capsule is the caudal.

The movements are free. In elevation the clavicles can be brought in contact with each other; in depression they are carried below the horizontal position. Protraction and retraction are free and approximately equal. Rotation is present but limited.

SHOULDER REGION

(Figs. 18, 19)

This heading is used to include the lateral end of the clavicle, the scapula, the proximal part of the humerus, the acromioclavicular joint and the shoulder joint. They will be discussed in order.

The lateral end of the clavicle is relatively simple. Its cephalic surface is nearly flat and smooth; the caudal has a large *subclavicular fossa.* The lateral surface is the *acromial articular facet.*

The *scapula* is of the quadruped type rather than the human. It is convenient to describe it in terms of a dorsolateral surface, a costal surface, a vertebral border, an axillary border, a cephalic border and its three angles.

The dorsal surface is crossed from the vertebral border to the lateral angle by the strong *scapular spine.* The spine is continued laterally well beyond the lateral angle as the *acromion.* The latter is bent near its termination so that the acromial articular surface faces medially. The spine divides the dorsal surface into a quadrilateral supraspinous fossa and a triangular infraspinous fossa. The costal surface is made up largely of the subscapular fossa which is deepest at its lateral end. In the younger specimens the vertebral border is rather evenly convex, in the older it approaches a straight line for more than half its length.

The greater part, about the cephalic three fourths, of the axillary margin is formed by two ridges separated by a fossa. This is rather sharply cut off from the caudal fourth, which is thin.

At the lateral end of the cephalic border is a heavy *coracoid process*, separated, in the younger animals, from the lateral angle by an epiphyseal line. It begins with a short, thick base, then bends sharply to be directed ventrally and caudally.

The most interesting structure at the lateral angle is the *glenoid cavity*. This is suboval in shape with its base toward the axillary margin. Its shape might best be said to be the result of blending a larger circle with a smaller ellipse. Just above it is a small smooth *supraglenoid tubercle*, and just below a larger rough *infraglenoid*.

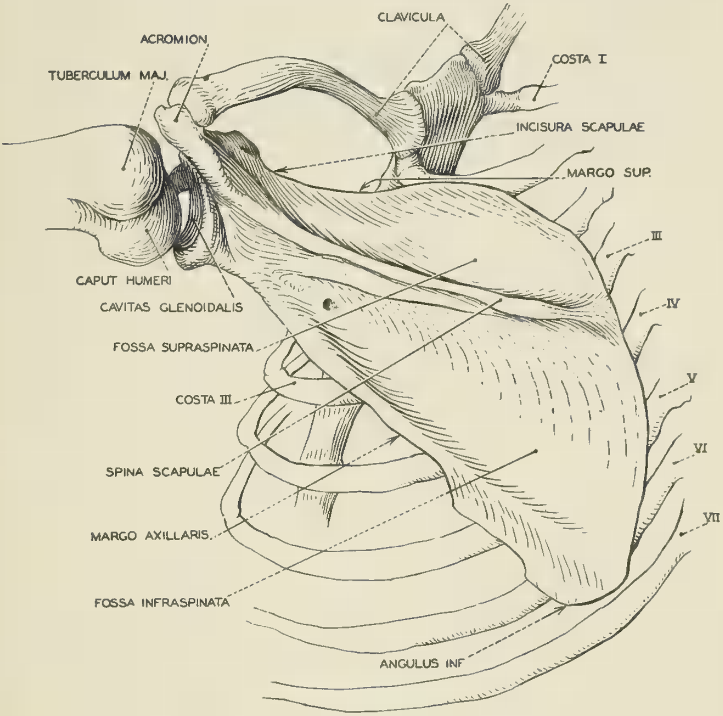

FIG. 18. The left shoulder girdle, posterior view. The clavicle articulates more with the dorsal surface of the sternum than is indicated in the drawing.

The proximal end of the humerus has the head, the neck, the greater and lesser tuberosities and their crests, the intertubercular sulcus, and the deltoid crest. In the younger specimens there is a proximal epiphysis formed by the head and the two tubercles and separated from the shaft by a common epiphyseal line. The line apparently disappears last in the region of the head.

The *head*, caput humeri, is a little less than a hemisphere and for the most part is directed dorsally. Both tuberosities are large and separated by a deep sulcus. The crest of the *greater tuberosity* (tuberculum majus), which is distinctly marked, forms the anterior margin of the shaft in its proximal third. The *deltoid crest* occupies a position just proximal to the middle of the lateral surface. As in the case of the scapula it may be said that the proximal end of the humerus approaches the quadruped rather than the human type.

Acromioclavicular joint

This is a rather simple diarthrosis with nearly flat surfaces and a loose capsule. The only ligament readily demonstrable is the *coracoclavicular.*

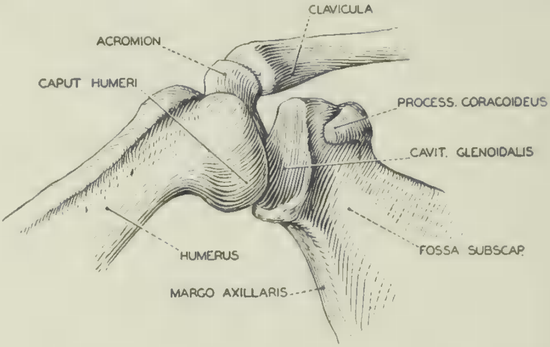

FIG. 19. The right shoulder region, anterior view.

This is a heavy fibrous band, some distance from the joint, from the base of the coracoid process to the dorsal margin of the clavicle.

The movements at the acromioclavicular joint supplement those of the sternoclavicular and shoulder joints. Rotation is freest. Rotation of the glenoid cavity upward is accompanied by elevation and retraction of the clavicle at the sternoclavicular joint. Rotation downward is accompanied by protraction and a slight depression of the clavicle. Abduction and adduction are present but rather limited.

Shoulder joint

The shoulder joint is a diarthrosis of the ball and socket type. As in man it is rather imperfect. The capsule is long and loose and the head of the humerus can be readily withdrawn from the glenoid cavity with the capsule intact. The *coracohumeral ligament* passes across the top of the joint from the base of the coracoid process to the greater tuberosity. On its dorsal surface the capsule is reinforced by a thin sheet from near the base of the ventral margin of the acromion. The intertubercular sulcus lodging the long head of the m. biceps brachii is bridged by a *transverse ligament.*

The fact that the glenoid cavity consists of a larger and a smaller segment has been mentioned earlier. It may be said that the medial margin of the glenoid is notched. Bridging this notch is a structure comparable to the *labrum* of man. It begins on the supraglenoid tubercle and ends on the infraglenoid. The result is a symmetrical articular surface on the scapula. This ligament is separated from the rest of the articular surface by a synovial recess.

Movements at the shoulder joint. Flexion and extension are fairly free, but are usually accompanied by movements of the shoulder girdle before reaching 45°. Generally it appeared that flexion was about 90°, extension 45°, abduction 80°, adduction somewhat less, but the distal end of the humerus could be carried across the ventral midline of the body. Medial and lateral rotation fall just short of 90°. Starting from the anatomical position medial rotation exceeds lateral by about 10°.

ELBOW REGION

(Fig. 20)

This region includes the distal end of the humerus, the proximal ends of the radius and ulna, the elbow joint and the proximal radio-ulnar joint.

The distal end of the humerus consists of the trochlea, the capitulum, the medial epicondyle, the lateral epicondyle, and olecranon, radial and coronoid fossae.

The *trochlea* or ulnar articular surface, which forms about two thirds of the distal articular surface, takes nearly the form of a truncated cone with the ventral surface interrupted by a low ridge. It has ventral, distal and dorsal surfaces. The *capitulum*, which articulates with the radius, is really condyloid in shape and has ventral and distal surfaces. The *medial epicondyle* may properly be described as a dorsomedial tuberosity. The *lateral epicondyle* is rough and is continued proximally as a well defined epicondylar line. On the dorsal face proximal to the articular surface is the deep *olecranon fossa*, on the ventral surface in a similar position are the shallow *coronoid* and *radial fossae.* The former is just above the trochlea, the latter just above the capitulum.

The younger animals will show at least two centers of ossification, a small one for the medial epicondyle, and a large one for the combined trochlea and capitulum.

The most striking structure at the proximal end of the ulna is the large *semilunar notch*, the articular surface for the humerus. This is in the form of a semicircle with raised margins except laterally. Immediately distal to this notch is a strong *coronoid process*. On the lateral surface at the level of the coronoid process is the *radial sulcus*, the articular surface which receives the head of the radius. This is made up of a large dorsal and a small ventral segment.

The proximal end of the radius is characterized by the capitulum and the radial tuberosity. The *capitulum* is essentially discoidal, presenting a concave proximal articular surface for the humerus and a circumferential articular surface for the ulna. The latter surface is broadest medially and narrowest laterally. The *radial* or *bicipital tuberosity* is a large elevation distal to the capitulum at the junction of the ventral and medial surfaces. In the recent condition it is overlaid by a bursa.

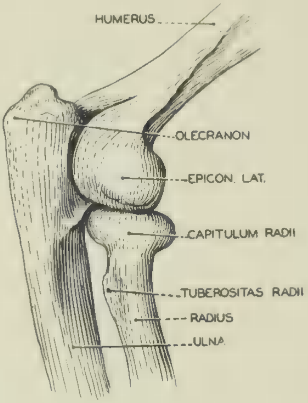

Fig. 20. The right elbow region, lateral view.

Elbow joint

The elbow and proximal radio-ulnar joints are enclosed in a common capsule which is thick except in its dorsal part. On the medial side there is an *ulnar collateral ligament* readily separable from the surrounding tissues. Its proximal attachment is to the distal end of the medial epicondyle, its distal attachment to the shaft of the ulna some distance from the joint. The lateral segment of the capsule is strengthened by the fibrous attachments of the radiodorsal muscles and a *radial collateral*

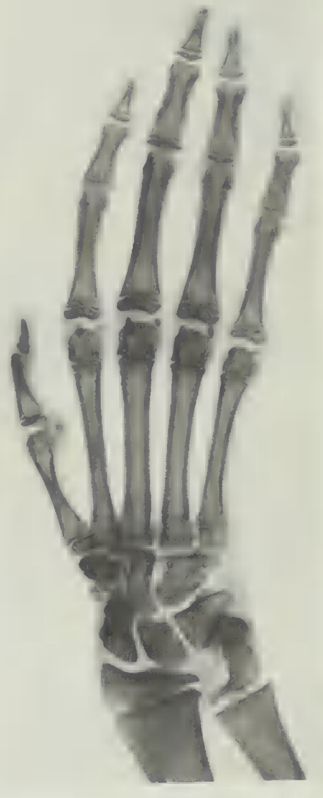

Fig. 21. The hand; roentgenogram of young animal.

ligament. This latter is not readily separable from the capsule or from the *orbicular ligament.* The latter, attached to either margin of the radial notch, almost completely encircles the head of the radius and provides an articular surface for it.

The movements at the elbow are flexion and extension. The former permits the front of the fore arm to be brought into contact with the front of the arm. In extension the arm and fore arm are almost in a straight line. During flexion the fore arm is carried medially; during extension laterally.

At the radio-ulnar joints pronation and supination equal or exceed 90°.

HAND REGION

(Fig. 21)

Under this heading are included the distal ends of the radius and ulna, the carpals, the metacarpals, the phalanges, and the intercalated joints.

The distal end of the radius is large and quadrilateral in section. There is a small articular facet on the medial surface, the *ulnar notch*, for the head of the ulna. The large distal articular surface, the carpal, is slightly concave and is continued onto the medial surface of the styloid process. This latter, the *radial styloid*, appears as a distal projection of the lateral margin. The dorsal and lateral surfaces have grooves for the tendons of the radiodorsal musculature. The structures just described, with the exception of the sulci, are separated from the shaft by an epiphyseal line in the immature animal.

The distal end of the ulna is small and relatively simple, presenting as points of interest two articular surfaces on the head, a styloid process and a sulcus. There is a *marginal articular surface*, circumferential, for the radius, and a *distal articular surface*, carpal. The dorsal segment of the bone is continued well beyond the distal articular surface as a cylindrical *styloid process.* This process has an articular surface. On the lateral surface between the head and the styloid process is a sulcus for the tendon of the m. extensor carpi ulnaris. The head and the styloid process are united with the shaft by a distinct epiphyseal line in the immature animal.

Carpal bones

(Fig. 21)

The carpal bones (ossa carpi) as seen in a roentgenogram are rather hard to interpret and when a direct examination is made of them it is found that the arrangement is somewhat complex. There are nine carpals and a sesamoid bone. There is a proximal row of four bones, a distal row of four, and an intermediate central bone on the radial side. In the proximal row the *navicular*, *lunate* and *triquetrum* occur in order from the radial to the ulnar side. The *pisiform*, which is relatively very large, lies volar to the triquetrum. It is of interest that the triquetrum has a large articular surface and the pisiform a small one for the ulnar styloid.

The distal row consists of the *hamate* on the ulnar side, then in order the *capitate* and *lesser multangular*. The row is bent at its radial end so that the *greater multangular* is volar rather than lateral to the lesser.

The *os centrale* is placed so that it articulates largely with the navicular of the proximal row and with the capitate and the two multangulars of the distal row. It has a small articular surface for the lunate.

There is a *sesamoid* on the volar surface of the greater multangular associated with the tendon of the m. abductor pollicis longus.

Metacarpal bones (fig. 21). These are five in number and require no special description. They are modified long bones and ossify as a shaft and one epiphysis, proximal in the first and distal for the others.

Phalanges (fig. 21). Again no detailed description is necessary. As in man there are two in the first digit and three in each of the other digits. They ossify as a shaft and a proximal epiphysis.

Sesamoid bones (fig. 21). Two sesamoids, a medial and a lateral are formed at each of the metacarpophalangeal joints. They vary somewhat in size.

Joints of the hand

There are here included the distal radio-ulnar, the radiocarpal, the intercarpals, the carpometacarpal, the metacarpophalangeal and the interphalangeal joints.

Distal radio-ulnar joint. This is between the head of the ulna and the ulnar notch of the radius. The joint is completely cut off from the radiocarpal by an articular disc. There is a strong dorsal radio-ulnar ligament which is in continuity with the disc. This joint together with the proximal radio-ulnar is for pronation and supination already described.

Radiocarpal joint. This diarthrosis is between the distal end of the radius, the articular disc just described with the radio-ulnar joint, and the ulnar styloid proximally, and the navicular, lunate, triquetrum and pisiform distally. It is a rather simple condylarthrosis with ulnar and radial collateral ligaments and an interosseous ligament from the ulnar to the triquetrum. The most interesting feature is that the ulnar styloid and the pisiform enter into the formation of the joint and that there is continuity with the cavity between the triquetrum and pisiform. Both of these bones articulate with the ulnar styloid.

The joint is essentially bi-axial, but a forced rotation can be demonstrated. Volar flexion is approximately 90°, dorsal about 45°. Ulnar flexion during supination approximates 60° and remains about the same during pronation. Radial flexion during supination does not exceed 30° and is slightly less during pronation.

Intercarpal joints. It does not seem necessary to describe the joints between the adjacent bones beyond saying that they are all diarthroses. Between the proximal and distal bones there is a continuous joint cavity variously named in man as the midcarpal or transverse carpal joint. In the rhesus monkey this can be best described by dividing it into a medial and a lateral segment. The medial joint, a condylarthrosis, is between the triquetrum, lunate and central proximally and the hamate and capitate distally. The long axis of this joint is transverse. The lateral joint is between the navicular and central proximally and the two multangulars distally. It may also be referred to as a condylarthrosis. Its long axis is dorsoventral. This midcarpal joint continues the movements of the radiocarpal joint, especially dorsal flexion.

Carpometacarpal joints. As in man the first of these permits the greatest range of motion. Flexion and extension are both relatively free. Abduction seems to be somewhat limited by the web between the first and second digits. Adduction permits the medial margin of the thumb to be carried dorsal to the dorsal surface of the hand. Rotation is present. It is possible to oppose the volar surface of the thumb against the palm of the hand. The second and third joints permit a very limited amount of movement. This is increased at the fourth and is quite free at the fifth for the dorsal and volar movements. The first may be described as a saddle joint. The others as irregular, although the fourth and fifth approach the condyloid.

Metacarpophalangeal joints. These are all bi-axial, permitting flexion, extension, abduction and adduction. In the first the dorsal and lateral movements are limited. In the others dorsal flexion equals or exceeds 90°, volar is in excess of 120°, and the lateral movements are free.

Interphalangeal joints. While these are all uni-axial joints it is to be noted that the distal joints of the second to the fifth digits permit dorsal flexion up to 90°.

PELVIS

(Fig. 22)

The pelvis of the rhesus monkey is long and narrow. In a pelvis at hand, if the greatest length is taken as 30 units, the greatest width of the major pelvis is 18, of the minor 14 and a dorsoventral at the level of the acetabulum is 12.

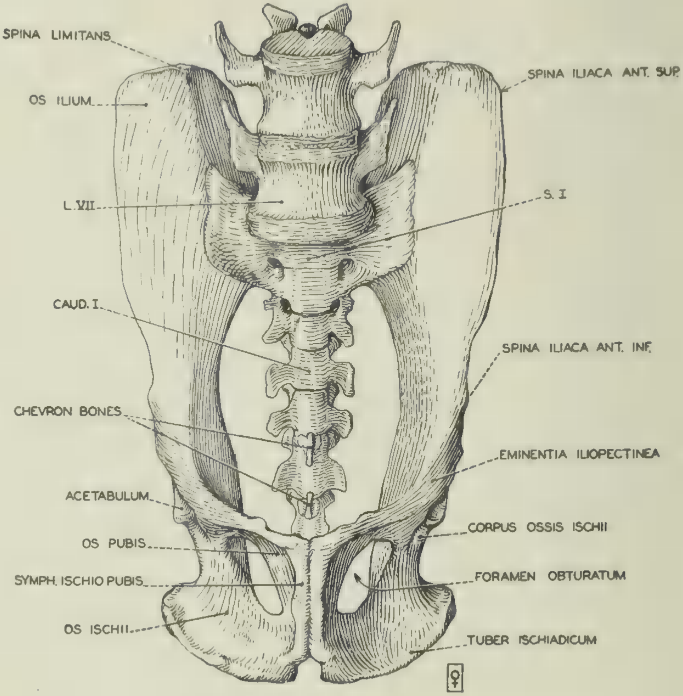

Fig. 22. The female pelvis, anterior view.

It is rather difficult to decide what the anatomical position of a monkey is and in the discussion that follows the pelvis is oriented on the basis that its long axis is essentially a continuation of that of the lumbar region of the vertebral column.

If the terminology of human anatomy be followed there is a major and a minor pelvis, but it must be recognized that the terms are incongruous, for the minor is much larger than the major. The cephalic aperture of the minor pelvis is elliptical or suboval and is bounded by the pubis ventrally and laterally, the ilium and ischium laterally, and the sacral and caudal vertebrae dorsally. The caudal opening is diamond shaped and bounded in its ventral half by the ischium, especially the tuberosities, and in the dorsal half by a thickened portion of the gluteal fascia. This latter, which runs from the ischial tuberosities to the caudal vertebrae, is apparently the equivalent of the sacrotuberous ligament.

The bones that form the pelvis are the sacral and caudal vertebrae dorsally, the ilium laterally, the pubis ventrally and the ischium caudally. The last three bones together with the acetabular bone form the os coxae.

Coxal or innominate bone

(Fig. 22)

This differs markedly from that of man, and approaches the typical quadruped form. Its chief characteristics can be seen in figure 22.

The elements forming this bone are here fused but it is readily seen that the *ilium* forms its cephalic two-thirds, the *ischium* the dorsal part of the caudal third, and the *pubis* the ventral. To this must be added a fourth bone, the *acetabular*.

The structures that require special description are the acetabulum, obturator foramen, ischial tuberosity, iliopectineal eminence, pubic crest, and the sacral articular surface.

The *acetabulum* is present as a deep fossa on the lateral surface. The pubis may not enter into its formation, its place then being taken by what may be termed an acetabular bone or bones. This is situated ventrally between the ilium and ischium. In one specimen the acetabulum appears to be formed by the ilium and ischium only. As in man, the acetabulum presents a lunate articular surface interrupted by an acetabular notch caudally and surrounding a fossa which is non-articular.

The *obturator foramen*, enclosed by the pubis and ischium, is large and ovoid with its base directed caudally. The *ischial tuberosity* forms the entire caudal surface of the bone and lies beneath the callosity. It is ovoid with its base dorsal. Cephalic to it along the dorsal margin of the bone is a shallow ischiadic notch. An *iliopectineal eminence* is present on the pelvic inlet at the iliopubic junction, which in the young animal is a synchondrosis. The symphyseal surface where the bones of the two sides join is long and pubo-ischiadic. The *pubic crests*, which form the ventral segment of the pubic inlet, end laterally in a small spine and are separated from each other by the *symphysis pubis*. The *sacral articular surface* is irregular and is partially separated into dorsal and ventral segments by a notch in its cephalic margin. The dorsal segment has the form of a truncated triangle with its long axis dorsoventral; the ventral is subelliptical with its long axis cephalocaudal.

The joints of the pelvis are the vertebral joints already discussed, the synchondrosis between the several elements of the coxal bone, the pubo-ischiadic symphysis, and the sacro-iliac. Only the last two need further discussion.

Pubo-ischiadic symphysis

The joint is rather complex and this description must be regarded as very incomplete.

What is here called the symphysis is long and narrow and may be readily divided into a *pubic segment* which is cartilaginous and an *ischial segment* which is fibrous. The pubic segment forms about one fourth of the entire union.

Several specimens were examined, and as they differ somewhat from one another each will be discussed.

Perhaps the average picture for the young animal is that in which the cephalic or pubic segment has hyaline cartilage continuous with that of the pubic crests. In the ischiadic segment the union is by fibrous tissue with the suggestion of a gelatinous matrix. At the extreme caudal end the union becomes wider and there is a more dense fibrous tissue. There is much fibrous tissue on the ventral and caudal surfaces of the joint.

In a young female there was a distinct longitudinal cleft in the middle of the cartilage of the pubic segment.

In a female that died during the latter half of pregnancy there were no marked changes in the pubic segment, but in the ischiadic segment the gelatinous structure was slightly accentuated. The change was not marked. No appreciable amount of relaxation could be demonstrated with the ventral ligament intact. In all females that were examined near term in the Carnegie Colony, this portion of the symphysis was found to be relaxed, however (Straus, 1932).

In an old female whose early history was unknown, but in whom there was no recent pregnancy, the pubic region was entirely different. A bony union was present between the two pubic bones. The cartilage, however, was not completely replaced, and it could be readily demonstrated in the ventral part of the joint.

In a young male there were a few vacuoles in the pubic segment.

Sacro-iliac joint

This is a diarthrosis with the opposed surfaces slightly irregular. There are strong cephalic, dorsal, caudal and interosseous ligaments. The dorsal are the strongest. In neither this nor the preceding joint was there enough movements to suggest that it was important. In the pregnant female near term, however, relaxation of this joint has been reported (Straus).

HIP REGION

Under this heading are included the acetabulum, the proximal end of the femur, and the hip joint.

The acetabulum has just been described with the pelvis.

The proximal end of the femur presents a head, the fovea of the head, the neck, the greater trochanter, the lesser trochanter, the intertrochanteric crest, the intertrochanteric line, the trochanteric fossa and the linea aspera.

The *head of the femur* is in excess of a hemisphere. The extent of the articular surface is greatest dorsally and least caudally. Dorsal to the center of the medial surface is a deep pit, the *fovea capitis*, in the depths of which in a specimen at hand are three nutrient foramina. The *neck* is thick, rather long and with the shaft forms an angle of 100°. Both the *greater* and the *lesser trochanters* are large. The former appears as a cephalic continuation of the lateral part of the shaft to end in a free tip which might well be called a coracoid process. The proximal extent of the great trochanter is greater than that of the head. The medial surface is deeply concave to form the *trochanteric fossa*. The femoral neck also takes part in the formation of this space. The lesser trochanter projects dorsomedially from the dorsal surface of the shaft just distal to its junction with the neck. Its base ossifies as part of the shaft, its apical segment as a separate center. The dorsal margin of the greater trochanter is continued distally as a heavy *intertrochanteric crest* which ends by blending with the lesser trochanter. The ventral margin of the latter ends distally in a rough tubercle. The *intertrochanteric line* is best seen on the medial surface ventral to the lesser trochanter and can be followed caudally to the linea aspera. It would seem much better to call it a spiral or sigmoid rather than an intertrochanteric line. The *linea aspera* is a longitudinal elevation at or lateral to the middle of the dorsal surface of the shaft. Proximally it divides to enclose a broad roughened area limited cephalically by the lesser trochanter and intertrochanteric crest. Distally there are also two limbs, one directed toward the lateral condyle, the other toward the medial epicondyle.

Hip joint

This is a multiaxial diarthrosis between the pelvis and the thigh. The osseous structures, acetabulum and femoral head, have already been discussed. The capsule of the joint is strong throughout and an *iliofemoral ligament* may be recognized. This appears as a broad, thick band at the junction of the anterior and superior segments of the capsule, spreading out over both.

When the capsule is opened it is seen that the articular surface is completed across the acetabular notch by a *transverse acetabular ligament.* The ligament also converts the notch into a foramen which connects the extracapsular region with the acetabular fossa. There is a *labrum* present which increases the extent of the articular surface except ventrally.

The line of reflection of the synovial membrane is for the most part at or near the junction of the head with the neck. Opposite the greater trochanter, however, there is an extension of the synovial sac, so that the membrane covers all of the neck as well as the medial surface of the trochanter at its junction with the neck.

The *ligamentum teres* is large and not at all round. It is in the form of a truncated triangle with a broad base attached to the acetabular fossa, the transverse acetabular liagment, and the bone ventral to the ligament. The distal attachment is to the fovea of the head. For the most part it is made up of synovial membrane, the segment from the acetabular ligament alone being fibrous. It is much longer than the interspace between the acetabulum and the femur, and apparently its only function is to carry the vessels of the femoral head.

While the joint is multi-axial, by far the greatest range of movement is around the transverse axis. Flexion permits the front of the thigh to be brought into contact with the anterior abdominal wall. In extension the longitudinal axis of the thigh becomes nearly parallel to the corresponding axis of the vertebral column.

The movements around the dorsoventral axis vary with the degree of flexion. In complete extension both abduction and adduction are rather limited. The range of both movements increases with flexion, but neither ever reaches 90°. Similar statements may be made for medial and lateral rotation, which of course occur around a longitudinal axis.

KNEE REGION

(Fig. 23)

In this region are included the distal end of the femur, the proximal end of the tibia, the proximal end of the fibula, the patella, the knee joint, and the tibiofibular joint. There is a sesamoid in either head of the m. gastrocnemius.

The distal end of the femur is much like that of man. There is a medial condyle, a lateral condyle, a patellar surface, an intercondyloid fossa, and a lateral and a medial epicondyle.

The articular surfaces are of most interest. The concave *patellar surface* is best seen in a ventral view, the convex condyles in a dorsal. All converge on the anterior part of the distal surface. The *lateral condyle* is slightly larger than the *medial* and the lateral segment of the patellar surface is a bit larger than the medial. The two condyles are separated by a deep *intercondyloid fossa.* The medial surface of the medial condyle and the lateral surface of the lateral condyle are rough and form the respective *epicondyles.*

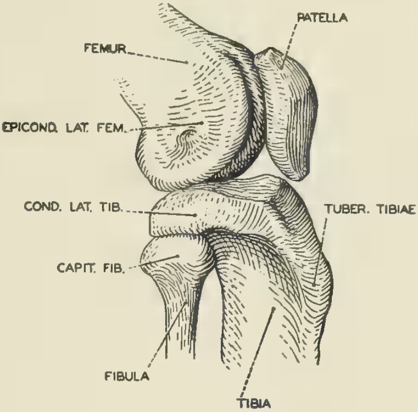

FIG. 23. The right knee region, lateral view.

The proximal end of the tibia is larger and is usually described as consisting principally of a medial condyle, a lateral condyle and a tibial tuberosity. The proximal surface on either side is a concave articular area for the femoral condyles. Between the two articular surfaces is an elevation, the intercondylar eminence, which is made up of the medial and lateral intercondylar tubercles. Ventral to the eminence is a larger shallow fossa, dorsal to it a small deep fossa.

On the distal surface of the lateral condyle is the flat, elliptical *fibular articular surface.* On the ventral surface at the junction of the shaft and the proximal end is a raised quadrilateral area, the *tibial tuberosity.* This may ossify as a part of the proximal end or have its own ossification center. The shape of the tibial shaft varies. In cross-section it is triangular at the proximal end, oval in the middle, and circular at the distal end.

The *fibula* is irregular. A flat elliptical articular facet marks the proximal end.

The *patella* lies as a sesamoid bone in the extensor tendon. It is ovoid in outline. The ventral surface is convex and non-articular. The proximal three-fourths of the dorsal surface is a sellar articular area, the distal fourth is non-articular. Just proximal to the patella the extensor tendon is organized in such a way as to suggest another sesamoid on manual examination.

Knee joint

This joint is very much like that of man. It is a diarthrosis, rather complex in structure and movement. The bones involved are of course the femur and the tibia.

The structures to be examined first are the articular capsule, the patellar ligament, the tibial and fibular collateral ligaments.

The *capsule* is strong except in its anterior part. The dorsal segment, which is thicker than the rest, is made up of oblique and irregular fibers. The oblique fibers are grouped as two ligaments, a broad medial and a narrow lateral. Proximally each is attached to the corresponding femoral condyle, distally they converge to the intercondylar region of the tibia.

The *patellar ligament* properly belongs with the extensor musculature.

The *tibial collateral ligament* crosses the medial surface of the joint somewhat obliquely. From its proximal attachment to the medial epicondyle of the femur it passes downward and forward to attach to the tibia on the medial surface near the anterior margin. It is a relatively broad band—more than 5 mm. The *fibular collateral ligament*, on the other hand, is narrow, less than half the width of the tibial, but is thick and can be readily demonstrated. From its proximal attachment to the lateral epicondyle of the femur it passes distally to the anterior surface of the shaft of the fibula just below the epiphyseal line. Just dorsal to this latter ligament is a broad thin segment of the capsule beneath which the proximal part of the popliteal muscle passes.

When the capsule is opened it is seen that the femur and tibia are not in direct contact, but that the medial and lateral menisci are interposed. In addition the anterior and posterior *cruciate ligaments* and the *synovial folds* are exposed.

The *medial meniscus* is in the form of a crescent open laterally: the *lateral meniscus* forms a complete ring. Both are concave on the femoral surfaces. The medial is the larger. From the junction of the dorsal and medial segments of the lateral meniscus a strong ligament passes to the medial surface of the medial condyle of the femur. This, which for convenience may be called the meniscocondylar ligament, is lateral to the posterior cruciate. The posterior cruciate ligament connects the lateral surface of the medial femoral condyle with the dorsal surface of the tibial intercondylar region. The anterior cruciate connects the anterior intercondyloid fossa with the medial surface of the lateral condyle.

The movement is similar to that in man though the rotation is not as marked. At the beginning of flexion there is a medial rotation, at the end of extension a lateral rotation. An adequate description would be rather long, but with a specimen in hand it is easy to observe what is taking place.

The knee can be flexed until the calf is brought into contact with the dorsal surface of the thigh. Extension falls just short of a straight line. When the foot is dorsiflexed extension is reduced. Both medial and lateral rotation are permitted in the flexed position, but are practically absent in the extended.

Aside from their more obvious function several statements should be made about the ligaments. The tibial collateral assists in limiting extension and lateral rotation and is carried forwards in medial rotation. Medial rotation is limited by the medial oblique popliteal ligament, the cruciates, and the meniscocondylar. Lateral rotation is limited by the capsule and external ligaments.

Proximal tibiofibular joint. This is a plane surface diarthrosis.

FOOT REGION

(Fig. 24)

Under this heading are included the distal ends of the tibia and fibula, the tarsals, metatarsals, phalanges and the joints between them.

The distal end of the tibia is a rather abrupt quadrilateral enlargement of the shaft. There are to be noted a medial malleolus, a distal articular surface, a notch for the fibula and several sulci for the tendons of cruropedal muscles. The *medial malleolus* is a continuation of the entire medial surface distally for three or four millimeters. Sometimes the anterior half extends beyond the posterior. Its lateral surface is articular. The *inferior articular surface* for the talus is concave from ventral to dorsal but convex from medial to lateral. Its cartilage is continuous with that of the malleolus. There are two sulci on the dorsal surface, one immediately adjacent to the malleolus, the other more lateral. The *fibular notch* occupies the lateral surface. In the recent condition it is filled with loose areolar tissue and fat.

The distal end of the fibula or the *lateral malleolus* at first sight looks much like the proximal end. More careful examination shows that the distal articular surface is distinctly medial while the proximal is nearly superior. Distal to the dorsal part of the former is a well marked fossa for the attachments of the talofibular and calcaneofibular ligaments. The distal articular surface forms a diarthrosis with the talus. Proximal to it is the tibial surface with no distinguishing character.

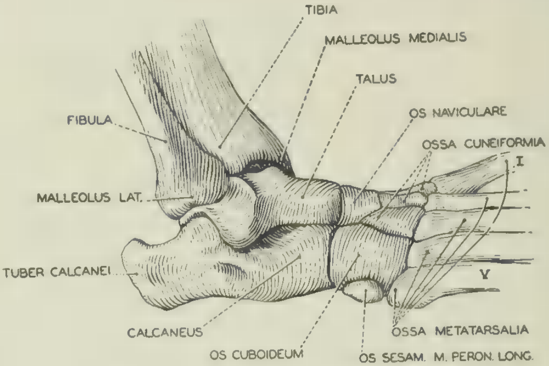

FIG. 24. The right foot, lateral view.

Tarsus

(Fig. 24)

The seven tarsal bones, talus, calcaneus, navicular, first, second, and third cuneiforms, and the cuboid form the proximal third of the foot. They are all irregular in shape.

The *talus* or *astragalus*, which articulates with the bones of the leg, may discussed in terms of a proximal segment, the body, an intermediate, the neck, and a distal, the head. Most of the body is articular. The upper surface is the tibial, the medial and lateral are malleolar, the plantar is the concave calcaneal. On the dorsal border is a sulcus (m. fl. digit. fib.) bounded on either side by a tubercle. The plantar surface of the neck is almost entirely a convex calcaneal articular area. The distal face of the head is a convex navicular articular surface. Its cartilage is directly continuous with that of the plantar surface of the neck.

The *calcaneus* or heel bone is the largest of the tarsals. On its dorsal surface are the three articular surfaces of the talus, and on the distal end one for the cuboid. From the junction of its dorsal and medial surfaces projects the sustentaculum tali. The proximal end of the bone is the calcaneal tuberosity. There is a bursa between the tuberosity and the calcaneal tendon. The plantar surface of the sustentaculum is grooved by the tendon of the m. flexor digitorum fibularis.

The *navicular* lies between the talus and the cuneiforms and the concave articular surface for the former covers the proximal surface of the bone. The distal end has two articular facets for the three cuneiforms. The more medial of these shows an indistinct separation into a plantar segment for the first cuneiform and a dorsal segment for the second. The lateral surface forms a diarthrosis with the cuboid, while the medial projects as a tuberosity.

The bones of the distal row, lying between the navicular and calcaneus proximally and the metatarsals distally, need no individual description. The first cuneiform has the shape of a boot. For the others the names are sufficiently descriptive and the several articular surfaces are indicated in the illustrations. There is a sulcus for a peroneal tendon on the plantar surface of the cuboid. In older animals at least, there is a sesamoid bone in the portion of the tendon of the m. peroneus longus that lies on the lateral surface of the cuboid. The distal articular surface of the first cuneiform is condyloid.

The metatarsals and phalanges need no separate description.

Distal tibiofibular joint

This is a synarthrosis which procures its strength from well developed ventral and dorsal ligaments. The interosseous space is filled with areolar tissue and fat. The dorsal ligament has an articular surface for the talus.

Talocrural joint

This is a trochlear diarthrosis between the bones of the leg and the talus. The articular surfaces include the distal surface of the tibia, the lateral surface of the medial malleolus, the medial surface of the lateral malleolus, the posterior tibiofibular ligament and the reciprocal surfaces on the talus.

The ligaments, which are many and striking, make the crurotarsal region suggest a morphologist's paradise. Some of them may be described.

The anterior and posterior tibiofibular ligaments have been discussed above.

The oblique tibiocalcaneal ligament passes from the medial surface of the medial malleolus distally and laterally along the dorsal and lateral surfaces of the neck of the talus to end on the dorsal surface of the calcaneus medial to the pulley for the common extensors. Closely associated with the proximal end of this is the transverse crural ligament, a broad flat band lying superficial to the extensor tendons just proximal to the malleoli.

The *tibiotarsal ligament* has its proximal attachment to the ventral part of the medial surface of the tibia as a single cord. As it passes toward the plantar surface it divides into a proximal limb attaching to the sustentaculum tali and a distal ending on the plantar surface of the navicular and cuneiforms. The *talotibial ligament* is a short wide band from the medial surface of the medial malleolus to the medial surface of the talus.

The *calcaneofibular ligament* has its proximal attachment to the distal end of the lateral malleolus and its distal to the lateral surface of the calcaneal tuberosity. The talofibular lies medial and slightly dorsal to the calcaneofibular. It passes from the tip of the lateral malleolus to the lateral tubercle of the talus.

The movements of this joint are for the most part dorsal and plantar flexion about a transverse axis. It is not a pure hinge as some rotation occurs.

Talocalcaneal joints

Structurally it is necessary to recognize two joints, a proximal and a distal, the latter capable of further subdivision. The proximal is between the bodies of the two bones, the distal involves the neck and head of the talus, the body and sustentaculum of the calcaneus and a strong fibrocartilage which fills the large interspace between the sustentaculum tali and the navicular. Both are subcondyloid diarthroses. There are medial and dorsal ligaments.

Transverse tarsal joint

Under this name are included the talonavicular and calcaneocuboid. Both are diarthrodial and approximate the condyloid type. The synovial cavities are continuous with each other and with that of the distal talocalcaneal joint.

Movements in the joints of the crurotarsal region. It has been already noted that dorsal and plantar flexion occur at the talocrural joint. Abduction and adduction are freest at the talocalcaneal joints with the talocrural as an accessory. Rotation is found in both the talocalcaneal and transverse tarsal joints. Inversion and eversion, the summation movements, involve all of these, with the talocrural playing a minor rôle.

Tarsometatarsal joints. The greatest range of movement is at the first, then follow the fifth, fourth, third and second in order. It is to be kept in mind that the digits of the hand and foot are very similar and that the thumb and great toe are in comparable positions. At the first tarsometatarsal joint, a condylarthrosis, flexion, extension, abduction and adduction are all present and rather free. There is a little forced rotation. The joints of the fourth and fifth digits permit a limited amount of flexion and extension.

Metatarsophalangeal joints. These are all condylarthroses permitting dorsal flexion, plantar flexion, abduction and adduction. In the first joint dorsal flexion is a little less than 90°, plantar is limited only by the contact of plantar surfaces. Rotation is rather freer than in the preceding joint. For the other digits plantar flexion is 135° or less; dorsal is about 45° with the interphalangeal joints extended, but 90° with them flexed.

Interphalangeal joints. The joint for the first digit is much like its metatarsophalangeal joint, but the range of movement is somewhat restricted.

For the other digits the proximal interphalangeal joints permit plantar flexion to about 135°; dorsal less than 45°. In the distal joints the two movements are about equal, in each case being in the neighborhood of 90°. In all of these joints lateral movements can be forced, as can a little torsion.

As a forced movement the plantar surface of the great toe can be brought into contact with the plantar surface of the foot as far as the lateral margin.

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Chapter VI

THE TEETH

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The teeth of *Macaca mulatta* show certain similarities to the teeth of man, not only in gross and microscopic anatomical features, but also in sequence of development and in number. Although the order of their eruption[1] through the jaw at certain periods of life is not always the same, the variations fall within limits narrow enough to enable one to draw certain conclusions as to the age of the animal.

The dental formula of the deciduous teeth (fig. 25) is as follows:

$$i\,\frac{2-2}{2-2};\quad c\,\frac{1-1}{1-1};\quad m\,\frac{2-2}{2-2} = 20$$

Still-born animals of a gestation period from 153 to 169 days show partial calcification, as indicated by roentgenographs, only of the deciduous incisors, canines and first molars. The calcification of the deciduous second molars and of the permanent first molars is just beginning (fig. 26). After the tenth day of extra-uterine life the four deciduous central incisors, two in each jaw, may be expected to erupt. Of seventeen cases examined, in one animal under one month of age the mandibular deciduous central incisors erupted through the gum at two days of age. In none of the others was there definite evidence of this degree of development until after the ninth day. During the first month of life, usually the deciduous central incisors erupt—rarely the lateral incisors.

Of fourteen animals between thirty and sixty days of extra-uterine life, four had all of the deciduous incisors and the deciduous first molars erupted. There was no evidence at this age of even the beginning of calcification of the permanent teeth. Roentgenographs of animals between thirty and forty days old show well developed calcification of all deciduous teeth. This ten day interval seems to be a period of less active dental development than the following one. But usually in animals at this age teeth other than the deciduous central and lateral incisors maxillary and mandibular—are not erupted (figs. 27, 28). Between forty and fifty days the deciduous canines and first molars may be expected to appear through the gum line. This was the case in half of the animals examined; in the other half the eruption was delayed until about the eightieth day of extra-uterine life. By the time that the animal is three months old the eruption of the deciduous sets of teeth usually is completed (figs. 29, 30). In a small proportion of animals the second molar did not appear until the fourth month.

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[1] See footnote 2, chapter II.

The dental formula of the permanent set of teeth (figs. 31, 15) is as follows:

$$I\,\frac{2-2}{2-2};\quad C\,\frac{1-1}{1-1};\quad P\,\frac{2-2}{2-2};\quad M\,\frac{3-3}{3-3}=32$$

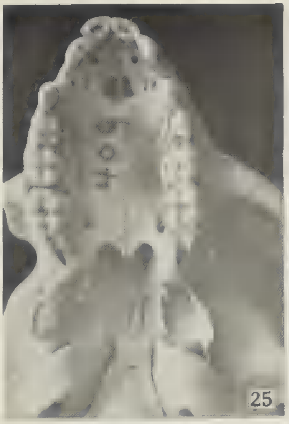
The calcification of the second set of teeth was not demonstrated roentgenographically until after the sixth month. At this time the permanent upper central incisors are just beginning to be formed.

At one year of age all the maxillary deciduous teeth have erupted and the formation of their roots is completed. The calcification of the permanent teeth has developed to the extent that the crowns of the central incisors show a clear roentgenographic outline of approximately one-third of the incisal portion (fig. 32). This extends further on the mesial and distal aspects of the crown than on the labial and lingual. The crown of the permanent first molar is calcified, but the outline of its roots is not demonstrated in the specimens until several months later. The tip of the mesiobuccal cusp is very near the gum line, but eruption of the tooth is delayed until the fifteenth month.

The mandible in animals one year old shows a dental development slightly in advance of that observed in the maxilla. The eruption and calcification of all deciduous teeth is complete even to the apices of the deciduous second molar and the deciduous canines (figs. 33, 34). Resorption of these roots does not begin until later. Both the permanent first and second molar may be demonstrated, but in the case of the second molar only the crypt, which contains the enamel organ and the dental papilla, is outlined.

The crown of the first molar is fully formed and the roentgenographs show a greatly thinned alveolar border over its mesial aspect. The mesiolingual cusp is usually in advance of the mesiobuccal and is the first to break through the gum.

No further dental development was observed until about the fifteenth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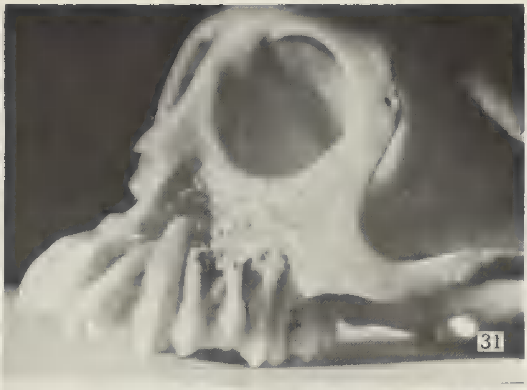
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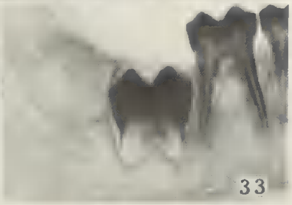
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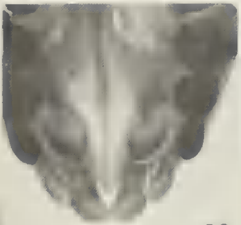
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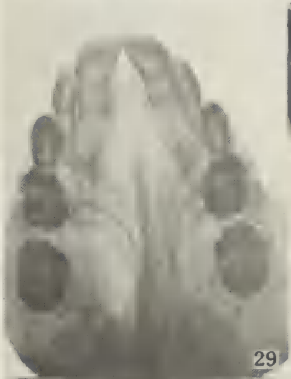
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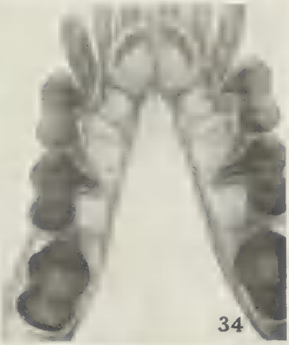
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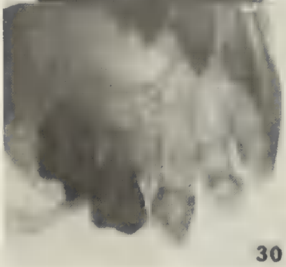
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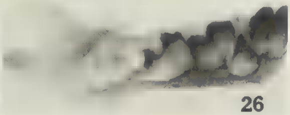
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Fig. 25. Deciduous dentition in the maxilla. The permanent first molars have also erupted. Age about 18 months.

Fig. 26. Deciduous dentition in mandible of animal one day old. The slight calcification of the first and second molars is indicated. (Fox No. 684; period of gestation unknown.) Roentgenogram.

Figs. 27 and 28. Nearly complete calcification of deciduous teeth in animal 32 days old (Carnegie No. 12; period of gestation 166 days). Roentgenograms.

Figs. 29 and 30. Complete calcification of deciduous teeth and nearly complete eruption at 88 days (Carnegie No. M). Roentgenograms.

Fig. 31. Permanent dentition, except for third molar, which has not yet erupted. (Compare fig. 15.)

Figs. 32, 33 and 34. Dentition of male one year and one day old (Carnegie No. F). Roentgenograms.

month, when the first permanent molars erupt. The crowns of the permanent incisors are nearly formed, but only the tips of the crowns of the permanent first and second premolars, canines, and second molars are calcified. The third molar is not demonstrable in the roentgenographs so early in life. At this same age the resorption of the roots of the deciduous teeth has advanced to include approximately half the root length.

There is a reasonable uniformity in the sequence of this process. The mandibular central incisors are usually the first to be shed; there then follow, in fairly regular order, the maxillary central incisors, the mandibular lateral incisors, the maxillary lateral incisors, the mandibular first molars, the maxillary first molars, the mandibular second molars, the maxillary second molars, the mandibular canines, the maxillary canines. There appears to be somewhat less regularity in the time of shedding the posterior deciduous teeth than of the anterior ones.

The time of eruption of the permanent teeth is nearly as regular as that observed in man. The first permanent tooth to appear is the first molar (about the fifteenth month); then follow the central incisors and the lateral incisors (sixteenth to seventeenth month); the first and second premolars (twenty-third to twenty-fourth month); the second molar (twenty-eighth to twenty-ninth month); the canines (thirty-first to thirty-second month); and finally the third molar. At two years of age, the calcification of the permanent teeth has progressed to such an extent that the roentgenographic outline of the incisors, both crown and root, is clearly shown.

The available data on animals between two and four years are somewhat fragmentary but indicate that the rate of formation of the crowns of the permanent teeth may vary to a slight extent. For example, in one animal exactly two years old, the permanent incisors were fully erupted and completely calcified; only the incisal half of the canine crown was calcified, as indicated roentgenographically. Thus in the nine months interval from fifteen months to two years the formation has been slower, apparently, than during other intervals of similar length. In another animal, aged four years and three months, one of the deciduous teeth, the maxillary right second molar, was still in place. The roentgenographs indicated that the permanent first molar, though fully formed, was unerupted. The permanent second molar likewise was unerupted, although the crown and half of the root were calcified. Exactly one year later, the same deciduous molar was still in place in spite of the complete eruption of all of the permanent teeth. This produced a faulty alignment of the teeth in the upper arch which resulted in a pronounced malocclusion.

Normally at five years the eruption and calcification of the permanent teeth is completed, but it is by no means unusual to find marked variations in their position in the jaw. In one animal six years old, the mandibular permanent canine had not erupted. In another the third molars, although calcified, were unerupted. In one of the nine year old animals all the permanent teeth were fully erupted except the third molar. This tooth was beginning to break through the gum line and half the root was calcified.

Dental examinations of animals of 10, 11, 12, 14 and 15 years indicate that the teeth are subject to dental caries and attrition. In caries the condition may progress to the formation of a chronic apical abscess. In attrition the crown may be worn away to the gum line. There is a corresponding recession of the pulp. There was no evidence either of erosion or of hypoplasia. A cleft palate was observed in one animal of unknown age.

The inclination of the teeth from the median line is exactly opposite from that observed in man. The crowns of all posterior maxillary teeth, instead of having a slight inclination toward the cheek as in man, show an axial direction toward the tongue. If a line be drawn through the long axis of the tooth it will not be parallel to the median line of the body, but the crowns will slope inward toward the median line. The roots, similarly, will diverge from it. All mandibular posterior teeth, if inclined at all, have an axial direction toward the cheek. The roots of the maxillary permanent central incisors normally curve into nearly an arc of a quarter circle. Their apices diverge from the median line and, lying in a plane nearly perpendicular to the long axis of the crown, point toward the nasopharynx.

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Chapter VII

THE MUSCULAR SYSTEM

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INTRODUCTION

Embryology. All musculature except the smooth muscles of the eye ball and of the skin glands are supposed to arise from mesoderm, although it is possible that this statement does not obtain entirely in the instance of the branchial musculature. In the dorsal part of the mesoderm develop the myotomes, which give rise to the dorsal division of the myomeric musculature (muscles of the back), while the remainder of the myomeric trunk musculature, as well as the smooth musculature of the viscera, develops from condensation of the lateral part of the mesoderm. The anlage of the limb muscles at first takes a sleeve-like form and also develops from condensation of the local mesoderm. Although there is no continuity with the trunk musculature in mammals, it occurs in fish; hence it seems necessary to assume that in higher forms the connection has been deleted from the embryological picture.

The originally segmental character of the myomeric musculature has been retained only in the instance of the intercostal muscles and the deeper part of the back musculature, but is suggested elsewhere, as in the m. quadratus lumborum and the tendinous inscriptions of the m. rectus abdominis. In the majority of the body muscles the original segmentation is now indicated only by plurisegmental innervation.

Types. Muscles are usually grouped in three categories: Unstriated, cardiac, and striated. Perhaps a better classification is the following: (a) Unstriated or involuntary, usually visceral; (b) cardiac, consisting of specialized visceral muscle fibers, striated, but forming a network, and otherwise differing somewhat from striated skeletal muscle; (c) striated or chiefly voluntary visceral (branchiomeric), usually lacking muscle spindles; and (d) striated or voluntary somatic (myomeric), possessing muscle spindles. The branchiomeric musculature differs from the myomeric in that it represents phylogenetically the original gill or branchial equipment supplied by cranial nerves V, VII, IX, X (and XI), whereas the myomeric series is innervated by actual spinal nerve components. Voluntary muscles differ in the proportion of red and white fibers which they contain, the former apparently being capable of more prolonged activity than the latter, which are better adapted for quick, spasmodic movements. It is only with the voluntary musculature that the present chapter deals.

Structure. A gross muscular unit consists of an envelope of connective tissue (epimysium) enclosing aggregations of muscle fibers or fasciculi, each of which is separated from the others by fascial septa (perimysium). Each muscle fiber is composed of a number of parallel, contractile, cross-striated myofibrils enclosed by sarcolemma. The individual muscle fibers are separated from one another by connective tissue septa (endomysium). The epimysium of the fasciculi is eventually attached, at either end of the muscular unit, to tendinous fibers by which the muscle is anchored.

Form. Muscles have various forms, such as quadrilateral, triangular, rhomboid, fusiform, unipennated, bipennated, multipennated, etc., in accordance with their shape and the manner in which their fibers are attached to terminal tendons. A muscle must have a relatively fixed base from which to operate, termed origin, and a movable point of attachment at the opposite end termed insertion, although not infrequently one of these may be as motile as the other, and the two points may be reversed physiologically under certain conditions. Origin, usually from the periosteum of bone but frequently also from cartilage, ligament, fibrous raphe and (rarely) skin, may be either fleshy (as in m. vastus intermedius) or tendinous. In the latter case the attachment of the muscle fibers may be by aponeurosis, in the form of diffuse tendon fibers in a broad, thin sheet, or gathered together in a stout, round tendon. Only rarely is there a narrow tendon of origin (m. soleus) but the tendon of insertion is frequently long. Some muscles show great conservatism in regard to their attachment, apparently being incapable of migrating from one bone (as the occipital) to another, while others exhibit well marked migratory trends.

Fascia. The all-pervading connective tissue which binds together the structures of the body is termed fascia. In some places, as where it covers the individual muscles, it occurs as thin, transparent, and somewhat elastic sheets; in others, as where it forms retinacula for the confinement of tendons, it is thickened and non-yielding. The subcutaneous fascia is usually considered as occurring in two layers, a superficial and a deep. In practice, it is not always possible, however, to be sure whether an additional stratum should not be recognized. The fascia superficialis, also termed panniculus adiposus where it contains a deposit of fat, is a sheet of areolar tissue investing the body, containing the ramifications of the cutaneous nerves and vessels, and rather closely adherent to the skin, although less so in the rhesus macaque than in man. It seems to be potentially divisible into two layers, which are likely separated by the development between them of the m. panniculus carnosus, a part occurring superficial and a part deep to that muscle sheet. Fat cells may occur in both layers, although this deposit appears always to be much more scanty than is sometimes encountered in man.

The fascia profunda is devoid of fat and forms the intimate investment of the muscles, between many of which it passes to constitute the intermuscular fascia or septa. It is anchored to such bony prominences as the vertebral spines and in the fresh specimen exhibits a laminated character in that parts of it may be artificially divided into several tenuous, transparent sheets. The deep fascia also contributes to the formation of retinacula and strong bands for the confinement of tendons to the digits, as well as investing membranes for the tendons themselves.

Nerve-muscle relationship. The relationship of a muscle to its nerve supply is fixed within narrow limits. As one sees it grossly a segmental nerve may have any composition. The nerve trunk itself is not necessarily of fundamental diagnostic importance, but the contained axons, and even more particularly the motor cell bodies within the central nervous system from which these arise are the critical elements in determing nerve-muscle relationship. Thus there may be some variation in the particular nerve trunk which supplies a muscle, but it is believed that the relationship between a muscle and its particular motor nucleus remains forever constant, throughout both ontogeny and phylogeny. This involves a slight modification of the so-called Rolleston-Fürbringer theory. In other words, it appears most probable that no matter how far a muscle may wander from its original myomeric position its relationship to the particular neurons by which it was primarily innervated remains constant. Excellent instances of the way in which a migrating muscle will carry along its original nerve are furnished by the mm. diaphragma, panniculus carnosus, and the facial muscles. There is no satisfactory evidence that a muscle can actually relinquish its original nerve-supply and assume a secondary or heterotopic innervation from a new source. Apparent exceptions to the Rolleston-Fürbringer theory may be explained by the fact that nerve fibers do not always follow the same paths, particularly through the limb plexuses, in reaching the muscle that they supply; hence it is believed that the innervation always furnishes dependable criterion for the determination of muscle homology, although the facts are occasionally obscured.

Muscle action. The contraction of striated muscle may be of a character either voluntary or involuntary, or both, as illustrated by the actions of breathing and of swallowing. The contraction of single muscles results in the approximation of their insertions toward their origins, but very few actions are accomplished by single muscles. Useful muscular action usually involves the contraction of a number of muscles which work by groups, and in extreme labor almost all the muscles of the body may contribute to the result. This is particularly the case around a ball-and-socket joint such as that of the hip, where each muscle must play some part in directing movement into the desired plane, keeping the joint in position and maintaining the posture of the body. Such actions are so complicated as to defy exact analysis.

Action of particular muscles or groups of muscles is either dynamic or static. Dynamic work is accomplished by some particular muscle group (as extensors) acting as synergists in prime movement while their antagonists relax to permit the movement or contract slightly to control it. Static work is accomplished by contraction of muscles for fixation of movable points to prevent undesired motion. In all muscle action the tone, affecting the elasticity of the muscles, is an important factor, and its inhibition in antagonists is a necessary accompaniment of efficient synergic action. No decisive muscular action occurs without utilizing all these factors. In addition there is involved the composition of the muscle, in regard to its proportions of red and white fibers, the inertia (weight of the parts) to be overcome, the lag of the neuromuscular impulse and of the resultant action, the fact that a muscle may be inhibited for one of two actions, both of which it appears well fitted to perform, and the imperfectly understood factor which makes an ape much stronger than a man.

Differences in position may change the action of a muscle so that it accomplishes extension instead of flexion, or vice versa, and a relatively slight shift in its origin or insertion may do the same, although group action of muscles is essentially conservative. For example, the short muscles about the hip in man have a somewhat different action than their homologues in a quadruped. It should also be realized that the same muscle group which in the primitive tetrapod posture, with laterally sprawling limbs, accomplishes extension of the thigh, may with propriety be considered as flexing that segment in a mammal. It is nevertheless strongly felt that the terms extensors and flexors should be retained throughout the vertebrates for those groups of muscles which are innervated respectively by the dorsal and ventral components of the plexuses.

An extensive exposition of the action of the muscles of the macaque has no place in the present volume, but it is felt that a brief statement of muscle action is highly desirable. This has been determined not only by a study of the muscles themselves, but also by the electrical stimulation under anaesthesia of the motor cortex of the cerebrum, and by stimulation of many of the peripheral nerves. In some instances, as in the hand and foot, however, it has been necessary to base the statements of muscle action on knowledge of the functions in man, with such modifications as appear to be indicated.

Muscles of the Head

Muscles of the eye (see chapter XVIII)
Facial musculature (see chapter VIII)
Muscles of the tongue and the pharynx (see chapter IX)
Craniomandibular musculature

CRANIOMANDIBULAR MUSCULATURE

The craniomandibular muscles are closely related genetically, being derived, together with the anterior belly of the digastric and the mylohyoid, from the mandibular arch musculature.

M. MASSETER (fig. 35). Superficially this appears to be double, with distinct origins. The more superficial part arises from the lower and inner surfaces of the anterior half of the zygomatic arch; it inserts upon the angle of the mandible and its entire lateral surface (exclusive of the coronoid process) and extends dorsally for two-thirds of the distance to the condyle and rostrally for about one centimeter beyond the angle. This part is robust. The second or deeper division arises from the lower and inner surfaces of the posterior two-thirds of the zygomatic arch; the posterior portion inserts upon a depression at about the center of the lateral surface of the ascending ramus of the mandible, while the anterior part fuses with the more superficial division.

M. TEMPORALIS (fig. 35). This is a thick, powerful muscle, which arises from the entire temporal fossa of the skull, its extent increasing with age until it finally approaches the midsagittal line. It is usually fused, at least in part, with the m. masseter in the region of the zygomatic arch, so that some of its fibers take origin from the inner surface of the latter. The fibers pass beneath the zygomatic arch to insert: (1) By a heavy tendon upon a slightly defined process at the base of the coronoid process near the last molar tooth and fleshily on the anterior part of the inner surface of the ascending ramus of the mandible, and (2) by a strong, broad tendon upon the coronoid process and the incisura

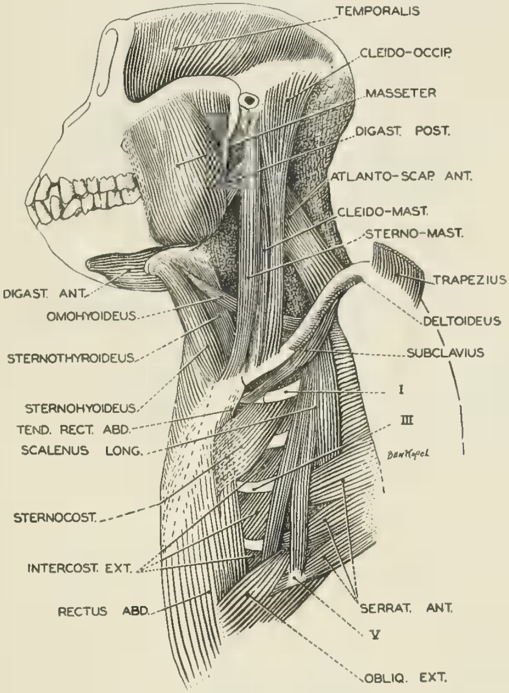

FIG. 35. Muscles of the head, neck and thorax. The facial and pectoral muscles have been removed. Left lateral view.

mandibulae. The muscle may exhibit at least partial separation into two layers, the more fleshy, superficial layer contributing largely to the formation of insertion (1), the deeper, more tendinous layer to insertion (2).

M. PTERYGOIDEUS EXTERNUS. This arises by two heads: (1) an upper from the infratemporal crest and fossa of the outer surface of the sphenoid bone, and (2) a lower from the outer surface of the lateral lamina of the pterygoid process. The two heads join to insert upon a depression just below the mandibular condyle on the inner surface of the ascending ramus.

M. PTERYGOIDEUS INTERNUS. This arises from the inner surface of the lateral lamina of the pterygoid process. Most of the fibers pass backward and downward to insert upon the angle and posterior part of the ascending ramus of the mandible.

Nerve-supply: The mm. masseter, temporalis and both pterygoidei are innervated by muscular branches (of the n. masticator) accompanying the mandibular division of the n. trigeminus.

Action. The craniomandibular musculature accomplishes the act of mastication. In clinching the incisor teeth the masseter is mostly used, and in apposition of the molars both that division and the temporalis. Protraction of the jaw is brought about by contraction of the pterygoids (chiefly external) with the assistance of the masseters; retraction by the posterior part of the temporalis and digastric, assisted mostly by the mylohyoid. Grinding movements of the jaw are effected by alternate action of the pterygoids of either side and synchronous action of the temporal and masseter muscles of the same side.

Comparative anatomy. The masseter, temporal, and pterygoid muscles have differentiated from the adductor musculature of the primitive first branchial (mandibular) arch. The masseter and temporalis are clearly recognizable in all higher forms. The pterygoids are probably derived from the original masseter complex, and the internal pterygoid in turn has given rise to the m. tensor tympani (see chapter XVIII). The m. tensor veli palatini also has common derivation with the masticatory muscle complex. The craniomandibular musculature is subject to considerable variability in respect to the degree of development of its several components, and in the occasional presence of more or less discrete accessory muscular slips.

MUSCLES OF THE NECK

Laryngeal musculature (see chapter IX)
Superficial lateral group
Deep lateral group
Suprahyoid group
Infrahyoid group
Prevertebral group

SUPERFICIAL LATERAL GROUP

These are distinct entities, and are derivatives of the same complex that gives rise to the m. trapezius.

M. STERNOMASTOIDEUS (fig. 35). This muscle arises from the tip of the manubrium sterni and inserts upon the mastoid process of the temporal bone below the external auditory meatus.

M. CLEIDOMASTOIDEUS (figs. 35, 42). This takes origin, between the preceding muscle and the cleido-occipital, from the extreme medial part of the clavicle. The insertion is upon the mastoid process deep to the attachment of the sternomastoid.

M. CLEIDO-OCCIPITALIS (figs. 35, 42). Origin is from the clavicle just lateral to the cleidomastoid. It inserts upon the lateral two-thirds of the superior nuchal line of the occipital bone.

Nerve-supply: All three muscles are innervated by a branch formed by an anastomosis between the ventral ramus of n. cervicalis II and a division of n. accessorius.

Action. The superficial lateral group of neck muscles nod the head when the action is bilateral, or incline it ipsilaterally and rotate it contralaterally when the action is unilateral.

Comparative anatomy. This group is normally represented in man by a single m. sternocleidomastoideus, but the cleido-occipital portion not infrequently occurs. In some lower mammals the latter may immediately adjoin the border of the m. trapezius. In non-claviculate mammals the cleido-occipital and cleidomastoid portions may fuse caudally with the pectoral or deltoid muscles to form a m. cephalohumeralis.

DEEP LATERAL GROUP

The three scalene muscles are quite complex, and their relationships extremely close. They cannot be directly homologized with the three scaleni of man, and it is possible that the scalenus posterior of human anatomy is not represented in the macaque.

M. SCALENUS BREVIS ANTERIOR. This lies ventral to the brachial plexus. It arises from the transverse processes of the third to fifth cervical vertebrae and strongly from the large ventral lamina of the sixth. The insertion is upon the ventrolateral aspect of the cranial border of the first rib.

M. SCALENUS LONGUS (fig. 35). Origin is from the transverse process of the fourth cervical vertebrae (or in some cases from as high as the second). It inserts upon the lateral aspect of the cranial borders of the third to fifth ribs. The slip to the fifth rib is inconstant, and there may be slips which attach to the first and second ribs.

M. SCALENUS BREVIS POSTERIOR. This muscle lies dorsal to the brachial plexus. It arises from the transverse processes of the first to seventh cervical vertebrae. The slip from the atlas may be absent. Insertion is upon the dorsolateral aspect of the cranial border of the first rib.

Nerve-supply: The mm. scaleni are innervated by short branches of the ventral rami of the nn. cervicales; the m. scalenus longus also receives twigs from the upper nn. intercostales.

Action. The scaleni are lateral flexors, or really abductors, of the neck, and, when the neck is fixed, elevators of the ribs to assist in forced respiration.

Comparative anatomy. The mm. scaleni of man are usually three in number (anterior, medius, and posterior), although a fourth (minimus) frequently occurs. According to Forster (1916) the m. scalenus posterior occurs in no mammal other than man.

SUPRAHYOID GROUP

These four muscles are genetically heterogeneous, but are grouped together for topographic convenience. The stylohyoid and the posterior belly of the digastric are derivatives of the hyoid arch musculature and thus are related genetically to the facial muscles; the anterior belly of the digastric and the mylohyoid are derived from the mandibular arch complex together with the craniomandibular muscles; while the geniohyoid belongs phylogenetically with the muscles of the infrahyoid region.

M. STYLOHYOIDEUS. The origin of this slender muscle is by a tendon from the very low styloid process of the mastoid bone. It passes, partly deep to the posterior belly of the digastric, to insertion by a slender tendinous band upon the hyoid bone at the lateral margin of the sternohyoid muscle. In some instances the tendon is not attached to the hoid, but inserts solely upon the lateral side of the digastric tendon at the point where the latter becomes arcuate. The stylohyoid is not pierced by the tendon of the digastric as it is in man. *Nerve-supply:* A branch of n. facialis.

M. DIGASTRICUS (figs. 35, 56). Origin is exceedingly high upon the mastoid, actually from the lateral third of the occipital plane. It is slenderly fusiform and converges to a narrow tendon just medial to the angle of the mandible. This tendon passes in an arc anterior to the hyoid bone and is continuous with the digastric tendon of the other side. From the arcuate part of the tendon arise the muscle fibers of the anterior belly, parallel to the sagittal plane. The muscle fibers of the anterior bellies of the two sides are interrupted by neither cleft nor tendon. The insertion is upon the medioventral border of the mandible from the symphysis backward for a considerable distance. There is a tendency for the fibers of insertion to occur in two layers. In some specimens the deeper layer may take the form of a distinct Y-shaped division, the central element being a tendon along the midline from the hyoid bone, the muscular crura of the Y diverging from it laterorostrally to the mandible. *Nerve-supply:* The posterior belly receives a branch of n. facialis, the anterior belly a branch of n. mylohyoideus (mandibular division of n. trigeminus).

M. MYLOHYOIDEUS (fig. 56). It arises from the hyoid bone and the medial suprahyoid raphe, which is broader immediately anterior to the hyoid, so that here the fibers reach the midline. The muscle fibers extend laterorostrally to insert upon the medial surface of the body of the mandible toward the dental arch. Anteriorly there is attachment to the lower portion of the symphysis. The posterior border of the muscle is much the heavier. *Nerve-supply:* N. mylohyoideus (mandibular division of n. trigeminus).

M. GENIOHYOIDEUS (figs. 56, 60). This muscle lies deep to the preceding. It arises from the posterior part only of the medial suprahyoid raphe and from the medial half of the hyoid bone. Its fibers run sagittally, adjoining the midline, and insert upon the medial surface of the mandible near the symphysis. *Nerve-supply:* N. hypoglossus.

Action. The suprahyoid musculature elevates the hyoid bone as an accompanying action to deglutition, and also depresses the mandible when the hyoid is fixed. The stylohyoid aids in this fixation.

Comparative anatomy. The m. stylohyoideus tendon in mammals is variable in its insertion, in some cases being attached to the hyoid and in others to the intermediate tendon of the m. digastricus. In prosimians and many monkeys (and occasionally in man) it is not pierced by the digastric. The entire muscle may be absent.

The doubly innervated m. digastricus is subject to great variation in mammals. The intermediate tendon is present in most primates but its attachment to the hyoid bone is inconstant. The anterior bellies may meet in the midline, as in the macaque, or they may be broadly separate, as is normal in man. In the orang-utan the anterior belly is reduced virtually to the point of absence.

The m. mylohyoideus is a rather constant muscle but may occasionally exhibit fusion with the anterior belly of the digastric. The m. geniohyoideus may show similar connection with the muscles of the tongue.

INFRAHYOID GROUP

The four muscles composing this topographical group are closely related to one another phylogentically and are probably derived, together with the m. geniohyoideus, from the ventral portions of the upper cervical myotomes; hence they may be regarded as the cervical representatives of the m. rectus abdominis division.

M. OMOHYOIDEUS (figs. 35, 42). This narrow ribbon-like muscle arises from about the middle of the cranial border of the scapula. Emerging from between the mm. supraspinatus and subscapularis, it passes between the sternomastoid and scalene complexes. The muscle fibers insert upon a narrow tendon which is attached to the hyoid bone at the border of the m. sternohyoideus, to which its tendon may fuse. No tendinous inscription is apparent. *Nerve-supply:* Ansa hypoglossi.

M. STERNOHYOIDEUS (figs. 35, 56, 60, 88). This is the most superficial of the infrahyoid muscles and is in contact or fused inferiorly with its antimere. It arises from the craniodorsal border of the manubrium sterni and inserts upon the base of the hyoid bone. Origin may be partly from the second costal cartilage. There may be an indication of at least one tendinous inscription near origin. *Nerve-supply:* Ansa hypoglossi.

M. STERNOTHYROIDEUS (figs. 35, 60). This lies partly deep to the preceding muscle, and is slightly separated from its antimere. Origin is from the manubrium sterni deep to the sternohyoid, but fused for a space with the latter. Cranially it emerges from the lateral border of the sternohyoid and inserts upon the caudolateral border of the thyroid cartilage. There may be at least one tendinous inscription near origin. *Nerve-supply:* Ansa hypoglossi.

M. THYROHYOIDEUS (fig. 60). It arises from the inferior border of the thyroid cartilage and inserts upon the lateral part of the hyoid bone. *Nerve-supply:* N. hypoglossus.

Action. The chief function of the infrahyoid musculature is depression, and hence fixation, of the hyoid bone.

Comparative anatomy. The m. omohyoideus is occasionally absent in some mammals. It may have a clavicular origin. An intermediate tendon is frequently absent in primates, especially the monkeys. The m. sternohyoideus usually possesses a tendinous intersection in monkeys, and not infrequently in man. An intersection likewise is present frequently in the m. sternothyroideus. These muscles of the infrahyoid region are subject to a considerable degree of minor variation of no particular interest.

PREVERTEBRAL GROUP

These muscles are derivatives of the lateral portions of the cervical myotomes. The two recti are merely modified ventral intertransverse muscles.

M. LONGUS COLLI. This has a double origin: (1) From the bodies of the vertebrae from the fourth thoracic to the fourth cervical (or even as low as the sixth thoracic), and (2) from the ventral processes of the sixth to third cervical vertebrae, especially from the broad ventral lamina of the sixth. The fibers insert upon broad tendinous bands which are attached to the bodies of the first four or five cervical vertebrae. This muscle is extremely well developed.

M. LONGUS CAPITIS. This arises by fasciculi from the ventral transverse processes of the sixth to third cervical vertebrae, most strongly from the sixth. It inserts upon the basi-occipital bone.

M. RECTUS CAPITIS ANTERIOR. Origin is from the transverse process of the atlas. It inserts upon the basi-occipital bone posterior to the attachment of the m. longus capitis.

M. RECTUS CAPITIS LATERALIS. It arises from the transverse process of the atlas lateral to the preceding muscle, and inserts upon the lateral portion of the occipital bone just anterior to the attachment of the m. obliquus capitis superior. It is a stronger muscle than the rectus capitis anterior.

Nerve-supply: All four of these muscles receive short branches from the ventral rami of the nerves forming the cervical and brachial plexus.

Action. The prevertebral musculature nods the head and flexes the neck.

MUSCLES OF THE TRUNK AND TAIL

PECTORAL MUSCULATURE

The pectoral musculature constitutes parts of the ventral or flexor muscles of the upper extremity that have migrated onto the chest wall. The small m. subclavius is genetically a portion of the same group. The pectoral musculature proper is more complex than in man. It may be considered to be composed of two layers: (1) A superficial or major, and (2) a deep. The former is again divisible into capsular and sternal parts, the latter into minor and abdominal parts. From the deeper stratum the panniculus carnosus has been developed, and has spread secondarily over the dorsal portion of the trunk.

M. PECTORALIS MAJOR (fig. 36). The pars capsularis, which is entirely superficial to and separable from the pars sternalis, arises thickly from the claviculosternal joint and thinly from the manubrium sterni. The latter origin is reduced in some specimens. The pars sternalis arises from the midline along the entire length of the sternum, the fibers meeting those of its antimere. The fibers of the caudal part of the muscle are successively folded under, beneath the lower margin of the main sheet, and have a more or less separate insertion upon the humerus. The common insertion of the remainder of the pars sternalis, and all of the pars capsularis, is upon a broad, thin tendinous sheet attached to the anterior border of the intertubercular sulcus of the humerus below the capsule of the shoulder joint. Pars sternalis may exhibit partial splitting into two layers in that sternal slips may arise between the main mass of the sternal portion and the deeper m. pectoralis minor; these intermediate slips insert on the same level as the sternal portion. The pars sternalis exhibits various degrees of fusion with the opposing surface of the m. deltoideus.

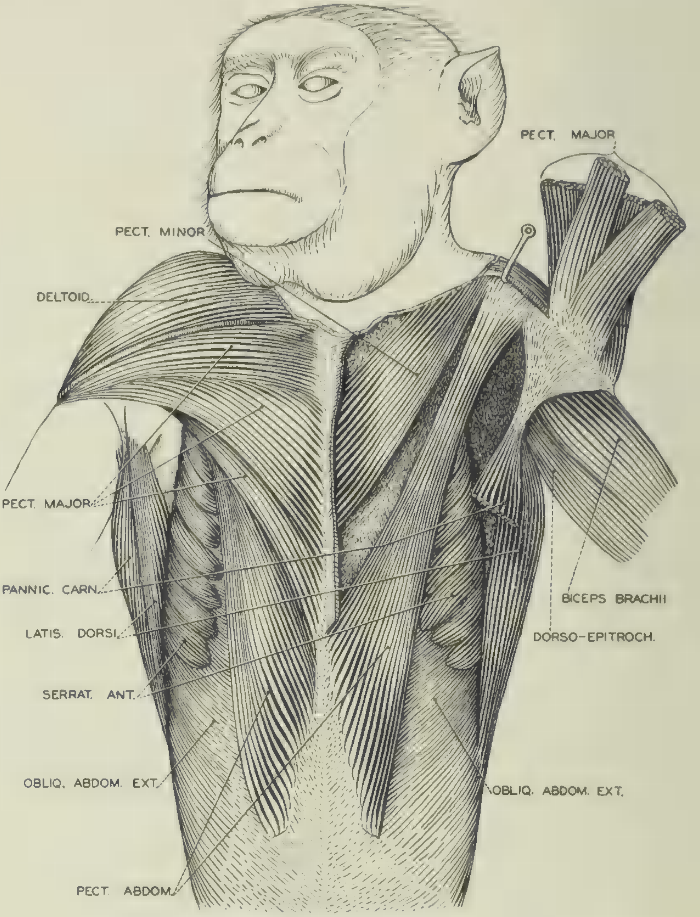

Fig. 36. Pectoral and abdominal musculature.

M. pectoralis minor (fig. 36). This usually arises from only the corpus sterni. The fibers run craniolaterally to insert upon the upper portion of an aponeurotic sheet that extends along the anterior border of the intertubercular sulcus of the humerus upward over the lesser tuberosity to the capsule of the shoulder joint. This aponeurosis lies deep to the attachment of the m. pectoralis major.

M. PECTORALIS ABDOMINALIS (fig. 36). The origin of this muscle is usually distinctly separated from that of the m. pectoralis minor by the length of the xiphoid process, although in some specimens the two muscles are practically continuous. Origin is for an extent of some 50 to 60 mm. from the sheath of the m. rectus abdominis caudalward of the xiphoid and lateral to the midline. Insertion is upon the humerus by means of the middle portion of the deep pectoral aponeurosis, continuous above with the insertion of the m. pectoralis minor, and below with the attachment of the m. panniculus carnosus.

M. PANNICULUS CARNOSUS (figs. 36, 37). This varies in its extent. It is represented by caudal and thoracic parts. The former arises from the superficial fascia over the anterior surface of the thigh and gluteal region and from the lumbar fascia lateral to the midline. Its ventral extent is not much beyond the midaxillary line. Its termination is along a fan shaped line across the dorsal and caudal part of the thorax, the fibers interdigitating with those of the thoracic portion. Along this line the fibers of the thoracic panniculus take origin, upward to a point just cranial to the axilla, a few bundles in this region usually being partly dissociated from the rest of the sheet. The fibers converge to the axilla, where they insert upon the humerus by means of a tendinous band which is prolonged into the lower portion of the deep pectoral aponeurosis. Just beneath the pectoral musculature proper the band is narrow and devoid of muscle fibers; it then broadens and becomes thinner.

M. SUBCLAVIUS (figs. 35, 42). This well developed, fusiform muscle arises from the lower and ventral border of the first costal cartilage, and inserts along the lower border of the middle three-fifths of the clavicle.

Nerve-supply: The m. pectoralis major is innervated by branches from the upper portion of the loop formed by the nn. thoracales anteriores lateralis et medialis; and the mm. pectoralis minor, pectoralis abdominalis and panniculus carnosus by branches from the lower portion of the same loop. The m. subclavius receives a separate nerve (n. subclavius) arising from the anterior division of the upper trunk of the brachial plexus (C5 and 6).

Action. The panniculus carnosus effects movement of the skin, but also helps the pectoralis major in depressing the arm from an elevated position. When the arm is depressed the latter muscle adducts the humerus. The pectoralis minor is mostly a depressor and inward rotator of the scapula, acting in antagonism to the trapezius and rhomboideus. The subclavius fixes the acromioclavicular joint.

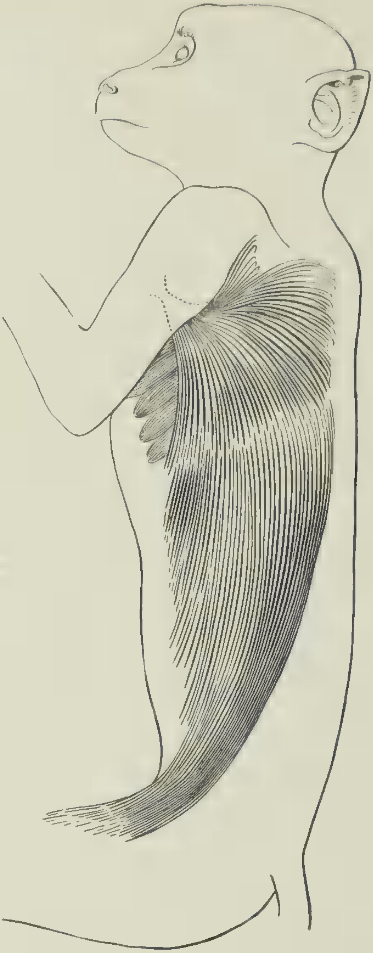

Fig. 37. The left panniculus carnosus. Digitations of the serratus anterior muscle are seen projecting beyond its anterior border.

Comparative anatomy. The pectoral complex in mammals represents at least two separate components of the primitive flexor musculature of the limb. The ectopectoral (or superficial) layer is composed of the division commonly termed m. pectoralis major, having in man three more or less distinct parts, with clavicular, sternal, and abdominal origins. The latter, however, is by no means homologous with the abdominal portion of the macaque and other mammals. The clavicular portion is reduced or absent in prosimians and monkeys, and in the orang-utan. In prosimians and monkeys the fibers of the two mm. pectorales majores regularly meet across the midline, whereas in the higher primates separation of the two muscles is the rule. The entopectoral (or deep) layer lies in a deeper plane and is composed of the m. pectoralis minor as usually defined, the m. pectoralis abdominalis of comparative anatomists, and the m. panniculus carnosus. In prosimians and monkeys the pectoralis minor usually inserts upon the humerus or the capsule of the shoulder joint; in the anthropoid apes and man the normal attachment is to the coracoid process. The mm. pectoralis abdominalis and panniculus are lacking in man, while the latter experiences progressive reduction in the higher primates. Certain abnormal tendinous and muscular slips occurring in the axillary region (such as the so-called "achselbogen") are probably vestiges, at least in part, of these two divisions. The m. subclavius is a part of the flexor musculature of the shoulder girdle that has become secondarily attached to the clavicle, but which, in non-claviculate mammals, is inserted upon the scapula.

THORACO-ABDOMINAL MUSCULATURE

Ventral division

This group is serially representative of the infrahyoid musculature above, both sets being derivatives of the ventral portions of the cervical and of the thoracic myotomes respectively.

M. RECTUS ABDOMINIS (fig. 35). The origin of this muscle is chiefly by two tendinous bundles, one from the manubrium sterni, the other from the lower border of the first costal cartilage opposite the m. cleido-occipitalis. Thence extends an aponeurosis, without further bony or cartilaginous attachments, giving rise to muscle fibers at the level of the third rib upon its lateral border and at the level of the fourth rib upon its medial border. The muscle fibers continue almost to the symphysis, insertion being by means of an aponeurosis upon the cranial border of the pubis for about two centimeters lateral of the symphysis. Ventrally the muscle belly exhibits an inconstant number of transverse tendinous inscriptions, there usually being two thoracic and from three to five abdominal inscriptions. The sheath of the muscle is formed by the aponeuroses of the external and internal oblique and transverse abdominal muscles. The aponeuroses of both oblique muscles pass superficial (ventral) to the rectus for their entire extent; the aponeurosis of the transverse abdominal courses deep (dorsal) to the rectus downward to a point about midway between umbilicus and pubis, where it passes ventrally to join the aponeuroses of the oblique muscles, thus giving rise to a linea semicircularis as in man. The tendinous fibers of the aponeurosis of the transverse abdominal may shift their position with respect to the rectus in sections, instead of at one point, so that there may be more than one semicircular line.

M. PYRAMIDALIS. This lies within the sheath of the m. rectus abdominis and is quite variable in size and attachments. Origin is usually from the cranial border of the pubis superficial to the insertion of the rectus, and insertion upon the linea alba at about the height of the linea semicircularis. The fleshy insertional fibers may extend above the latter point and pass uninterruptedly into those of the rectus.

Nerve-supply: Both m. rectus abdominis and m. pyramidalis are innervated by nn. intercostales and upper nn. lumbales.

Action. The rectus abdominis and pyramidalis strengthen the abdominal wall and the former especially is used in compression of the abdomen, as in defecation, in forced respiration, and in flexion of the trunk upon the pelvis or vice versa.

Comparative anatomy. The m. rectus abdominis represents the deep sheet of the ventral abdominal musculature; the m. pyramidalis the superficial sheet of primitive tetrapods, occurring in progressively reduced form in the marsupials and in the placental mammals, in many of which it is absent. The origin of the rectus primitively is from the first rib in prosimians and monkeys, but does not normally reach this height in the anthropoid apes and man. Tendinous inscriptions (occurring in most mammals) of a variable number, supposedly representing the primitive myosepta, are invariably found in the higher primates, but may be reduced or absent in some prosimians and monkeys. The tendinous sheath of the rectus, derived from the aponeuroses of the three lateral abdominal muscles, exhibits variation among primates. Above the linea semicircularis, the superficial layer of the sheath may be derived from the external oblique alone (as in prosimians and New World monkeys), from the external oblique and part of the internal oblique (as in man), or from the external oblique and the whole of the internal oblique (as in Old World monkeys and gibbons). Among primates the pyramidalis is absent in prosimians, in many monkeys and in some specimens of anthropoid apes and man. Its structure is extremely variable.

Lateral division

The musculature of this region is composed of three strata, derived from the lateral portions of the trunk myotomes, in addition to the m. quadratus lumborum of similar derivation. The external intercostals and external oblique are thus serially homologous and form the external layer, the internal intercostals and internal oblique the intermediate layer, and the transverse thoracic and transverse abdominal the internal layer. The sternocostal, and also the two posterior serrati and the levatores costarum of the back, are derivatives of the external layer and thus are related genetically to the external intercostals and external oblique. The subcostals, absent in the rhesus macaque but present in man, are merely extensions of the internal intercostals. In the neck the lateral musculature is represented by the scalene muscles.

M. STERNOCOSTALIS (fig. 35). This arises from the sternum opposite the second intercostal space by an aponeurosis which partly pierces and is partly fused with the aponeurosis of the m. rectus abdominis. The relations of the two tendons are complex and variable. The muscle fibers converge to a tendinous insertion upon the caudoventral border of the first bony rib just beneath the corresponding slip of the m. serratus anterior. *Nerve-supply:* A branch from the lateral division of n. intercostalis II.

MM. INTERCOSTALES EXTERNI (figs. 35, 61). These lie in the intercostal spaces and are eleven in number. Origin is from the lower border of the rib above, the fibers being directed caudosternally to insert upon the upper border of the rib below. The muscles (with the exception of the eleventh) extend from the region of the costal tubercles to within one to three centimeters of the midline. *Nerve-supply:* Nn. intercostales.

M. OBLIQUUS ABDOMINIS EXTERNUS (figs. 35, 36, 38, 40, 47). In the thorax this arises from the last nine ribs, origin from the fourth to the seventh being by a slender tendon from which the muscle fibers arise, deep to the serrations of the m. serratus anterior. The slips from the last four ribs interdigitate with those of the m. serratus posterior inferior. Origin is also from the lumbodorsal fascia just lateral to the extensor spinae musculature. The fibers are directed caudomedially. Insertion is by a tough aponeurosis that is separable from the underlying layers only to within about two centimeters of the midline, where it fuses with the aponeurosis of the internal oblique to form the ventral layer of the rectus abdominis sheath. Cranially the muscle fibers reach the midline, but caudally they barely encroach upon the groin. The caudal border of the muscle is weak and is attached only to the dorsal fascia and the pubis, while between these regions there is but fascial connection with the underlying internal oblique. The external inguinal ring (fig. 70A) is relatively much larger in both sexes than in man, being two or three times the diameter of the spermatic funiculus in the male. There is no inguinal ligament, and the inguinal ring is devoid of any structure resembling the reflex ligament of man. The bony insertion is upon the pubis near the symphysis (pubic tubercle) and upon the iliopectineal line near the pubo-iliac junction, the lower border of the aponeurosis between these two points of attachment forming an arch beneath which the femoral vessels and nerves pass. *Nerve-supply:* Nn. intercostales and upper nn. lumbales.

MM. INTERCOSTALES INTERNI (fig. 35). These occupy the intercostal spaces and are eleven in number. Origin is from the lower border of the rib above, the fibers being directed caudodorsally to insert upon the upper border of the rib below. The muscles (with the exception of the eleventh) extend from the region of the angles of the ribs to the midline. *Nerve-supply:* Nn. intercostales.

M. OBLIQUUS ABDOMINIS INTERNUS (figs. 38, 47). This arises from the lumbodorsal fascia in common with the external oblique (in relation to whose fibers it runs fairly at a right angle), from the lower margin of the thorax (the last two or three ribs), and from the acetabular border of the ilium. Cranially the muscle fibers extend toward the midline no farther than the level of the tip of the eleventh rib, but toward the groin they continue quite to the lateral border of the m. rectus abdominis. Insertion is chiefly by an aponeurosis which fuses with that of the external oblique (and below the linea semicircularis with that of the transverse abdominal also) about one or two centimeters lateral to the midline and passes superficial to the rectus abdominis, to reach the linea alba. Attachment is also by a thin aponeurosis upon the superior ramus of the pubis deep to and extending lateral to the attachment of the external oblique. The lower fibers continue downward in the male partly to form the cremaster muscle. *Nerve-supply:* Nn. intercostales and upper nn. lumbales.

M. CREMASTER (figs. 38, 70A). This arises as a continuation of the internal oblique and transverse abdominal muscles, with lesser attachment to the pubis. It surrounds the spermatic cord and the testicle. It is a much more powerful muscle than it is in man. *Nerve-supply:* External spermatic branch of n. genitofemoralis.

M. TRANSVERSUS THORACIS. This muscle lies upon the deep surface of the ventral thoracic wall. It is composed of six fleshy slips which arise from the dorsal aspect of the sternum and xiphoid process. Insertion is upon the cartilages of the second to seventh ribs, but the lower slips may insert in fascia between the ribs. The four upper slips run laterally and cranialward, the two lower laterally and transversely or slightly caudalward. *Nerve-supply:* Nn. intercostales.

M. TRANSVERSUS ABDOMINIS (figs. 38, 48). This arises from the deep sheet of the dorsal fascia which emerges from between the m. quadratus lumborum and the intrinsic back musculature. The direction of the fibers is just caudal of medialward. Cranially it is attached to the inner rim of the cartilaginous border of the thorax. Dorsally there is tough, tendinous attachment to the anterior superior spine of the ilium, while in the groin along its caudal border the weak transversus fascia is fused with the stronger one of the internal oblique. Toward the midline the muscular extent of the transversus layer coincides almost exactly with that of the external oblique, except that caudally muscle fibers continue to the region of the external inguinal ring and contribute to the formation of the cremaster muscle. The transversus inserts by means of an aponeurosis into the linea alba. This aponeurosis forms the deep layer of the rectus sheath downward to a point about midway between umbilicus and symphysis, at which point it abruptly passes ventral to the rectus muscle, to fuse with the aponeuroses of the internal and external oblique muscles, forming a linea semicircularis. The transition may occur in more than one stage, additional semicircular lines thus being formed. *Nerve-supply:* Nn. intercostales and upper nn. lumbales.

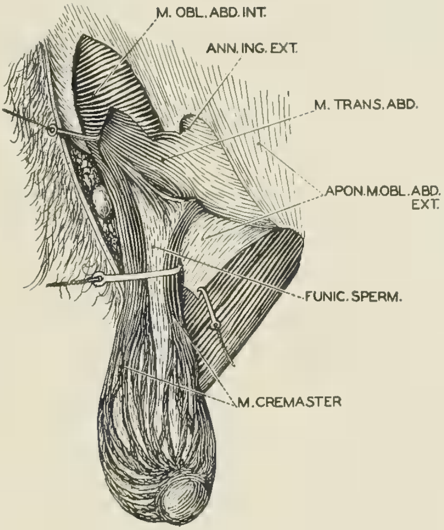

Fig. 38. Dissection of the right inguinal region of an adult male, showing the cremaster muscle.

M. QUADRATUS LUMBORUM (fig. 48). Origin in both fleshy and tendinous, from the medioventral aspect of the ilium between the anterior superior spine and the ventral portion of the sacro-iliac articulation. The fibers of origin intermingle with those of the m. iliacus, but in general occupy a deeper plane. The tendon, almost hidden by muscle fibers, passes cranially, giving rise all along its length to muscle fibers which insert upon the transverse processes of the seventh (slightly), sixth, fifth and fourth lumbar vertebrae. Another tendon arises from the transverse process of the seventh lumbar vertebra, its fibers inserting upon the transverse processes of the three upper lumbar vertebrae and upon the last two or three ribs. *Nerve-supply:* Direct branches from the ventral rami of the nn. lumbales.

Action. The part which the intercostal muscles play in respiration is still a matter of controversy. It is probable, however, that the external group and the interchondral part of the internal expand the chest during forced inspiration and the remainder of the internal fibers, assisted by the transversus thoracis, are used in forced expiration. The lateral abdominal muscles strengthen as well as compress the abdominal cavity, depressing the thorax and elevating the diaphragm so as to be of marked aid in forced expiration. They are brought into play in vomiting and defecation. Unilateral action deflects the hips,—an action which is useful in climbing as well as running. They flex the trunk upon the pelvis or vice versa. The cremaster elevates the testicle.

Comparative anatomy. In prosimians and both groups of monkeys the attachments to the iliac crest of the three lateral abdominal muscles are slight, their iliac origins being limited chiefly to the acetabular border. In the anthropoid apes and man these muscles are extensively attached to the crest. A true inguinal ligament is present only in man and gorilla. The origin of the external oblique may extend upward to the second rib or even to the first rib in lower primates. Tendinous intersections occur more frequently in the internal oblique than in the external oblique. Such intersections, supposedly representing vestiges of the primitive myosepta, are found in many lower mammals.

A sternocostal muscle (or muscles) occurs in most mammals. There are two in some prosimians, but only one in monkeys. This muscle is normally lacking in man and the anthropoid apes. The transverse thoracic muscle is usually composed of fewer slips in man than it is in the macaque.

Diaphragm

The diaphragm is a strong membranous and muscular partition separating the abdominal viscera and the enclosing peritoneum from the pericardium and pleura which enclose the thoracic viscera. It is dome-shaped, with convex surface directed cranially, so that by its contraction the abdominal viscera are compressed and the pleural cavities, and hence the lungs, expanded. It arises ontogenetically from the ventral portion of the fourth (and fifth) cervical myotomes, its anlage undergoing a caudal migration.

M. DIAPHRAGMA (fig. 61). Origin is chiefly from the inner margin of the ventral border of the thorax by a thin aponeurosis which is separable from the transversalis fascia only with difficulty. Peripherally the diaphragm is muscular, its fibers interdigitating to some extent with those of the m. transversus abdominis and converging to insertion upon a central tendon of semilunar shape, the concave part of which is directed dorsally. Upon this concave part is also inserted the two fibro-muscular crura, arising from (chiefly) the third lumbar vertebra and separated from each other by the hiatus aortica, for the passage of the aorta and thoracic duct. Near the ventral termination of the crura upon the diaphragm a strong muscle slip passes from the right to decussate with the fibers of the left crus, bridging a space (about 3 centimeters in length) which constitutes the hiatus oesophageus, for the passage of the oesophagus and the vagus nerves. At this point there is a thin though tough sheet of connective tissue extending from the caudal surface of the border of the diaphragm to invest the cardiac region of the stomach. A short distance to the right and ventral to the hiatus oesophageus is the smaller foramen quadratum, for the passage of the vena cava inferior. *Nerve-supply:* N. phrenicus.

Action. The diaphragm by its contraction increases the capacity of the thoracic cavity, compressing the abdominal viscera in the process, and so producing a passive protrusion of the abdominal wall. In quiet inspiration the diaphragmatic contraction is the chief active agent, with the thoracic walls largely held in position by tonic contraction of the intercostals. As respiration increases in vigor the true accessory respiratory muscles of inspiration (intercostals, mostly the external) are first called into action, and later those muscles having more remote effects in raising the ribs (scaleni, serratus anterior, sternocleidomastoid), thus increasing the thoracic capacity. Quiet expiration is accomplished by relaxation of the diaphragm, and forced expiration largely by contraction of the abdominal musculature aided by the intercostales interni, together with the transversus thoracis.

PERINEAL MUSCULATURE AND FLEXORS OF THE TAIL

The precise derivation of these muscles is problematical. For descriptive purposes they may be divided into two groups:

Perineal musculature
Flexor muscles of the tail

The perineal muscles are sometimes regarded as genetically, as well as topographically, related to the caudal flexors, but it is not altogether improbable that they form a portion of the sheet represented more cranialward by the rectus abdominis and the infrahyoid muscles.

The caudal flexor muscles occupy a hypaxial position, but there is no definite proof that they are serially homologous with the true hypaxial musculature of the trunk.

Perineal musculature—male

In the macaque, this musculature exhibits a pronounced sexual dimorphism, so that the two sexes must be considered separately.

M. SPHINCTER ANI EXTERNUS (figs. 71, 76). The fibers of this unpaired muscle encircle the rectum and end in the fibrous tissue of what corresponds to the midpoint of the human perineum, just ventral to the rectum, in common with the bulbocavernosus and the sphincter of the membranous urethra.

M. BULBOCAVERNOSUS (fig. 71). This extremely powerful muscle, together with its antimere, forms a kidney-shaped mass that embraces the urethra by encircling the corpus cavernosum urethrae, but not in part the corpora cavernosa penis as is the case in man. The two mm. bulbocavernosi are separated caudally by a median raphe, the urethra entering the middle of the common muscle mass and emerging from its cranial end. The muscle fibers arise from the raphe of the caudal aspect and insert upon the tough fibrous tunic of the urethra. Attachment dorsally is into the midpoint of the perineum.

M. ISCHIOCAVERNOSUS (figs. 47, 48, 71). This is a well-developed, bulbous, hemispherical muscle arising from a spinous process upon the extreme caudoventral part of the ischial tuberosity. Muscle fibers from this largely tendinous origin diverge chiefly in a ventral direction to firm insertion upon the fibrous sheath of the corpus cavernosum penis.

M. LEVATOR PENIS (figs. 48, 71). This is evidently a derivative of the preceding muscle. There passes a stout ligament from the ventral border of the ischium to the corpus cavernosum, and cranially bordering the m. ischiocavernosus. From near the ischial end of this ligament arises a slender muscle which extends parallel to the corpus cavernosum near its dorsal border. The muscle belly is short, but from it is prolonged a tendon. This shortly joins its antimere and the resultant common tendon accompanies the vessels along the dorsum of the penis and disappears in the skin of the prepuce.

M. SPHINCTER URETHRAE MEMBRANACEAE (fig. 71). This unpaired muscle surrounds the urethra just caudal to the prostate gland. Its fibers are attached to the midpoint of the perineum and to the puboprostatic ligament.

Nerve-supply: All five of the male perineal muscles are supplied by branches of n. pudendus.

Action. The sphincter ani externus closes the anal orifice. The bulbocavernosus compresses the corpus cavernosum urethrae in both micturition and ejaculation. The ischiocavernosus aids in the erection of the penis, while the levator penis raises it cranialward. The sphincter urethrae membranaceae closes the membranous urethra after micturition and during ejaculation.

Perineal musculature—female

M. SPHINCTER CLOACAE. The perineal musculature of the female exhibits much less differentiation into separate components than does that of the male. It assumes the form of an unpaired sphincter surrounding the external openings of the alimentary and urogenital tracts. Heavy muscle fibers pass from along the dorsal surface of the rectum and are continued forward, more weakly between ischial tuberosity and vagina, to end in an aponeurosis just ventral to the external urethral orifice. This muscular sheet is present on each side, and thus forms a common cloacal sphincter. This may give rise to a separate muscle bundle which superficially encircles vagina and urethra together, to a deeper vagino-urethral sphincter, and to superficial muscle bundles passing transversely across the perineum in the interval between rectum and vagina. There is sometimes present a muscle slip arising from the portion of the cloacal sphincter dorsal to the rectum, and passing obliquely to insert upon the ischial tuberosity. Muscle fibers completely encircling the rectum, and thus forming a m. sphincter ani externus, are always recognizable, although this muscular element is usually quite weak on the ventral side of the alimentary canal. The other aforementioned derivatives of the common cloacal sphincter are, however, exceedingly variable in respect to attachment and degree of development.

M. ISCHIOCAVERNOSUS. This arises from the ventral portion of the ischial tuberosity and inserts upon the crus clitoridis. It is usually but poorly developed, at times being represented by only a few muscle fibers.

Nerve-supply: The cloacal sphincter (and its derivatives) and the ischiocavernosus are both supplied by branches of n. pudendus.

Action. The sphincter cloacae complex constricts the genito-excretory and anal orifices, while the ischiocavernosus aids in the erection of the clitoris.

Comparative anatomy. The perineal muscles appear primitively (both phylogenetically and ontogenetically) in the form of an undifferentiated cloacal sphincter (much as in the female macaque), and the separate perineal muscle components are derivatives of this originally simple mass. Whereas the perineal musculature of the female macaque exhibits a primitive and only slightly differentiated arrangement, that of the male closely approaches the human condition. The chief differences in the males of these two forms consists in the presence in man of two additional muscular components (the superficial and deep transverse perineal muscles) and the accompanying loss of the levator penis element.

Flexor muscles of the tail

M. FLEXOR CAUDAE LONGUS (fig. 39). This robust muscle arises, just lateral to the caudal artery, from the ventral surface of the sacrum as high as the promontorium, and in some instances from the body of the last lumbar vertebra as well. It passes into a tendon that inserts by more or less distinct slips upon the ventral surfaces of the caudal vertebrae.

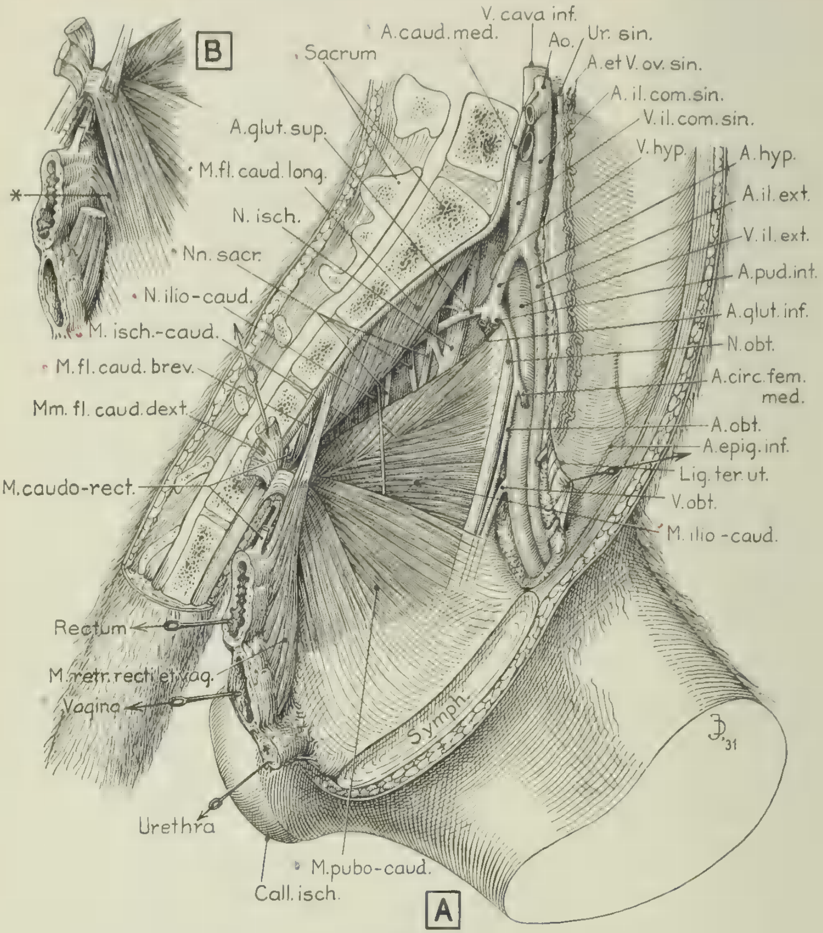

FIG. 39. Dissection of the left pelvic floor of an adult female, showing the flexor muscles of the tail. In B, the middle portion of the retractor muscle of the rectum and vagina has been removed, to show the rectal insertion of the pubocaudalis muscle. (Drawn by James F. Didusch.)

M. FLEXOR CAUDAE BREVIS (fig. 39). This is a much smaller muscle than the preceding. Origin is just medial to the long caudal flexor from the ventral surface of the last (third) sacral or the first caudal vertebra, or from both. It inserts upon the first chevron bone (between the second and third caudal vertebrae) and is also continued caudally into the common flexor tendon.

M. PUBOCAUDALIS (fig. 39). Origin is aponeurotic from the entire length of the inner surface of the symphysis and from the iliopectineal line dorsalward to about the region of the junction of ilium and pubis (to the point where the obturator nerve and vessels disappear). Muscle fibers shortly appear, and these converge chiefly to an insertion upon the lateral and ventral surfaces of the tail in common with the m. iliocaudalis; some of the fibers, however, usually pass ventral and slightly cranial to those of the iliocaudalis to insert upon the more proximal caudal vertebrae. Usually, but not invariably, some of the more ventral fibers insert not upon the tail but upon the dorsal aspect of the rectum.

M. ILIOCAUDALIS (fig. 39). This arises fleshily from the inner surface of the ilium as far ventrally as the iliopectineal line, and along the latter from the dorsal border of the m. pubocaudalis practically to the sacroiliac joint. The fibers converge to insertion upon the tail in common with the m. pubocaudalis, attachment being into the lateral and ventral sides of the third caudal vertebra and into the chevron bones, with continuation into the common caudal flexor tendon. In some specimens mm. iliocaudalis and pubocaudalis are distinctly separate until close to insertion, but in other examples the only cleavage between the two muscles is that produced near origin by the obturator nerve and vessels, which run across the pelvic surface of the former, and then pass deep (external) to the m. pubocaudalis.

M. ISCHIOCAUDALIS (fig. 39). This lies chiefly dorsal to the m. iliocaudalis. Origin is fleshy, from the rudimentary ischial spine and from the adjacent portion of the ischium, and insertion is upon the ventral sides of the transverse processes of the first three caudal or upon the last sacral and first two caudal vertebrae.

Nerve-supply: The long and short caudal flexors are both innervated by short direct branches from the ventral portions of the nn. sacrales and upper nn. caudales. Mm. pubo-, ilio- and ischiocaudalis are all innervated by direct branches from the ventral rami of nn. sacrales I and II.

In addition to the striated muscles herein discussed, the macaque possesses two muscles composed entirely of smooth muscle fibres, and which pass between the viscera and the tail (fig. 39). The paired smooth *m. retractor recti* (*m. retractor recti et vaginae* in the female) arises from the ventral surface of the first caudal vertebra and inserts into the rectum (and vagina in the female). It may be absent on one or both sides. The unpaired smooth *m. caudorectalis* passes from the dorsal part of the rectum in the midline to insert upon the ventral surface of the tail in the region of the second, third or fourth caudal vertebra.

Action. The caudal flexor muscles, when used bilaterally, depress the tail; when used unilaterally they both abduct and flex this member. The flexores longus et brevis are pure flexors, the pubocaudalis and iliocaudalis are abductor-flexors, and the ischiocaudalis is a pure abductor. The pubocaudalis also elevates the rectum.

Comparative anatomy. The long and short caudal flexors have retained their primitive origins from the vertebral column, whereas the three remaining elements of this group have migrated laterally onto the pelvic bones and have assumed the partial function of abductors of the tail. In those primates lacking an external tail the long and short flexors are reduced to functionless vestiges (represented in man by the m. sacrococcygeus anterior and by at least a portion of the anterior sacrococcygeal ligaments), or they may even be entirely absent. The ventral portion of the pubo-iliocaudal complex gains new attachments to certain of the pelvic viscera (particularly the rectum), while the remainder of this complex retains its original attachment to the reduced caudal skeleton and likewise inserts upon adjacent ligamentous structures. In this way the pubic and iliac portions of the original caudal abductor-flexor musculature gain partially new attachments coincident with the loss of the external tail, and form a m. levator ani (as of man). In such forms they no longer have the function of abduction and flexion of the bony tail (which is now practically immobile), but by union across the midline they form a hammock for the pelvic viscera. In the lower primates (as is the rule in lower mammals) the pubo-iliocaudalis complex normally has no attachment to the pelvic viscera; but occasionally in New World monkeys as well as in many Old World monkeys (as usually in the macaque) the rudiments of such a modification are present. In the anthropoid apes and man, all of which lack an external tail, a true m. levator ani occurs. The so-called arcus tendineus of the levator ani of man has been formed by disappearance of its muscle fibers along the pelvic brim (iliopectineal line). The m. ischiocaudalis (also termed m. coccygeus) exhibits a marked phylogenetic tendency toward reduction to a tendinous structure. The smooth m. retractor recti and m. caudorectalis undergo reduction in the higher primates. In man the former is represented by the m. rectococcygeus, while the latter is apparently entirely lacking.

MUSCLES OF THE BACK AND THE EXTENSORS OF THE TAIL

Extrinsic (superficial) group

The muscles composing this group are of diverse origin. None of them belongs to the true back musculature but they all have secondarily migrated onto the dorsal surface of the body. They are here grouped together merely for the purpose of topographic convenience. The trapezius is derived from the same sheet as the sternocleidomastoid complex, and hence is at least partly of branchial origin; the latissimus dorsi, rhomboids, and atlantoscapulars are genetic parts of the extensor musculature of the superior extremity, while the posterior serrati are derived from the external layer of the lateral division of the thoraco-abdominal musculature. These superficial muscles of the back, purely for descriptive purposes, may be regarded as constituting three layers. The superficial layer is composed of two muscles which cover most of the back,—the trapezius above and the latissimus dorsi below. The intermediate

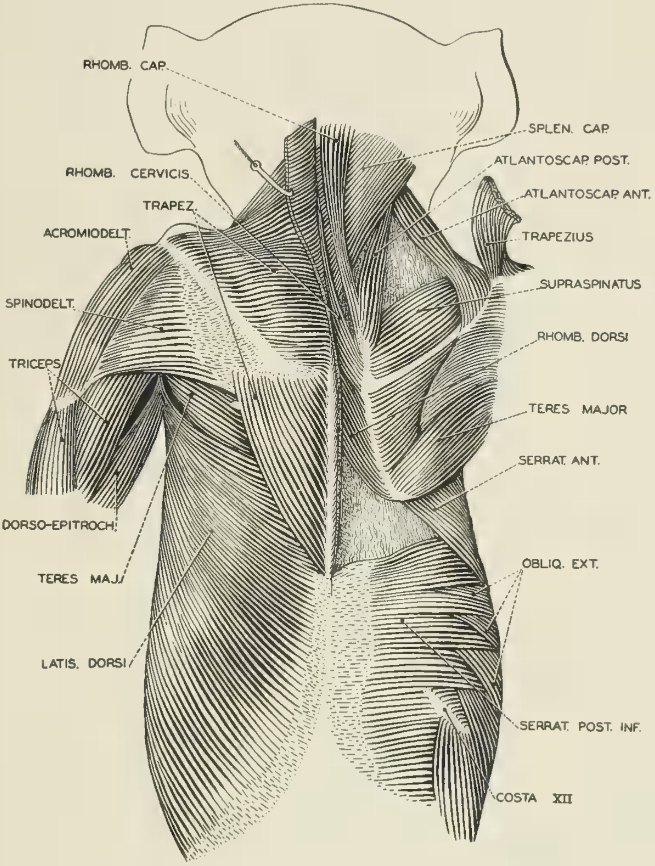

FIG. 40. The superficial or extrinsic back muscles. On the right side, the trapezius and latissimus dorsi muscles have been removed, exposing the deeper extrinsic back musculature.

layer is confined to the upper portion of the body, and is composed of the rhomboids and the atlantoscapulars. The deep layer, represented by the posterior serrati, extends over the major portion of the trunk, forming a more or less continuous muscular or fibrous sheet.

√M. TRAPEZIUS (figs. 35, 40). Origin extends from the occipital bone just forward of the inion along the vertebral spines to the tenth thoracic vertebra. A narrow part originating from the cervical extent of the midline and inserting upon the acromion and the extreme lateral part of the clavicle may be entirely separable from the thoracic portion of the muscle. The degree of this separation is variable. At insertion the caudal half of the pars cervicalis overlaps the cranial border of the remainder of the muscle. The latter is continuous, and inserts by an aponeurosis which is attached to the entire cranial border of the scapular spine, excepting only the tip of the acromion, and to the caudal border for a lesser extent. *Nerve-supply:* Branches derived from anastomoses between n. accessorius and nn. cervicales II, III and IV.

M. LATISSIMUS DORSI (figs. 36, 40, 42, 43). This arises from the spinous processes of the sixth to the eleventh or twelfth thoracic vertebrae and from the lumbodorsal fascia to a point about midway between the last (twelfth) rib and the crest of the ilium. The muscle fibers converge in a thick sheet to the axilla, where they split into two portions. The smaller and more dorsal division is continued as a tendon which joins the m. teres major, while the larger and more ventral portion is inserted by a tendon into the posterior border of the intertubercular sulcus of the humerus adjoining the m. teres major. *Nerve-supply:* N. thoracodorsalis.

M. RHOMBOIDEUS (figs. 40, 43). This is composed of three parts, usually clearly separable from each other, but the degree of independence is somewhat variable. (1) Pars capitis is a slender slip that arises from the median part of the superior nuchal line of the occipital bone medial to the m. cleido-occipitalis. It inserts between the pars cervicis and the m. atlantoscapularis posterior upon the vertebral border of the scapula opposite the scapular spine. (2) Pars cervicis, broader than the preceding, arises from the ligamentum nuchae and inserts upon the vertebral border of the scapula for the cranial half of the distance between the scapular spine and the glenovertebral angle. (3) Pars dorsi arises from the midline, continuing caudally from the pars cervicis to the level of the sixth or seventh thoracic spine. It inserts, continuous with the cervical portion, upon the vertebral border of the scapula for the caudal half of the distance from scapular spine to glenovertebral angle. *Nerve-supply:* All three rhomboid portions receive branches from n. dorsalis scapulae.

M. ATLANTOSCAPULARIS POSTERIOR (fig. 40). This muscle (also termed m. atlantoscapularis superior) arises from the more dorsal part of the transverse process of the atlas adjoining the m. atlantoscapularis anterior. It passes as a thin ribbon of muscle just beneath the m. trapezius to a tendinous insertion upon the vertebral border of the scapula just cranial to the scapular spine. Here it lies dorsal to the cranial insertion of the m. serratus anterior. *Nerve-supply:* A branch from n. cervicalis IV.

M. ATLANTOSCAPULARIS ANTERIOR (figs. 35, 40, 43). This muscle (which may also be termed m. atlantoscapularis inferior) arises from the ventral border of the transverse process of the atlas adjoining the m. atlantoscapularis posterior. It inserts strongly along the cranial margin of the lateral half of the scapular spine and the acromion as far as the acromioclavicular joint. *Nerve-supply:* Two or more branches from nn. cervicales III and IV.

M. SERRATUS POSTERIOR SUPERIOR. This is situated between the rhomboid layer and the intrinsic back musculature. It arises by an aponeurosis from the midline of the lower cervical and upper thoracic regions and extends laterocaudally. Muscle fibers develop about midway toward insertion, which is upon the caudal border of the second to fifth ribs, above the origin of the m. serratus anterior. *Nerve-supply:* Nn. intercostales I–IV.

M. SERRATUS POSTERIOR INFERIOR (fig. 40). This is an extremely variable muscle. It extends laterally and slightly caudally, lying deep to the m. latissimus dorsi in the same layer as the m. serratus posterior superior, with which it is usually connected by a sheet of rather tough fascia. Origin is from the superficial layer of the lumbodorsal fascia, and muscle fibers appear toward the lateral border of the extensor spinae musculature. Insertion is upon the caudal border of the ribs. In one extreme only the eighth and ninth ribs were involved, while in the other (illustrated) attachment was upon the last six ribs. *Nerve-supply:* Nn. intercostales of the spaces which are bridged.

Action. The trapezius acts in two parts; the cranial portion moves the scapula forward, while the caudal part adducts it. The latter function, for fixation, is used with great frequency. The latissimus dorsi is the chief retractor of the upper arm; it may rotate it somewhat medially. The rhomboideus, usually considered as the direct antagonist of the serratus anterior, is situated so as to adduct the scapula and, with the atlantoscapularis anterior, to move the vertebral border of the scapula in a cranial direction, and hence rotate the shoulder. The atlantoscapularis anterior moves the entire shoulder cranialward, while the atlantoscapularis superior merely tilts the vertebral border. The serratus posterior superior elevates the ribs and so assists in forced inspiration. The serratus posterior inferior can depress the ribs but probably acts chiefly in costal fixation.

Comparative anatomy. The trapezius sheet, including the sternocleidomastoid group, is the only muscular unit in the mammalian body invariably receiving both branchial and spinal innervation, and yet apparently incapable of division according to its nerve components. In some of the lower primates the spinous origin of this muscle does not extend as far caudalward as is usual in the anthropoid apes and man. Its clavicular attachment may be lacking, and this would appear to be a progressive feature. An occipital origin is usually absent in gibbons. Fusion of trapezius and latissimus dorsi sometimes occurs.

Origin of the m. latissimus dorsi from the crest of the ilium is also a progressive feature. This attachment occurs among primates only in man and the three great apes; in the former the connection with the iliac crest is relatively slight and aponeurotic, but in the three anthropoids the muscle arises fleshily from a considerable extent of the crest. The spinous origin is relatively reduced in the higher primates, especially in the chimpanzee and the gorilla. Costal origin is normally absent in prosimians and Old World monkeys. A scapular origin among primates is frequent only in man.

The m. rhomboideus is variable in structure. A pars capitis is regularly present in prosimians and monkeys, and is frequent in the orang-utan, but is commonly absent in the other anthropoids and man. The spinous origin of this sheet exhibits a tendency toward reduction.

The mm. atlantoscapulares (which may be single or double) are representatives of a levator scapulae element, and they may be considered as constituting the atlantic part of the serratus anterior sheet whose attachments at the shoulder have migrated. The atlantoscapular and serratus anterior muscles topographically form a primitively continuous sheet extending from the atlas on to the thorax. In the higher primates the atlantoscapular and the upper cervical portion of the serratus sheet persist to form the m. levator scapulae, while the lower cervical part disappears, limiting the serratus to the thorax. The so-called m. levator claviculae, which occurs in many monkeys and anthropoid apes, and which is found as a variant in man, is merely a part of the levator scapulae complex whose caudal attachment has migrated on to the clavicle.

The mm. serrati posteriores are quite variable. The inferior division is normally absent in the gorilla, and the superior is occasionally lacking in the orang-utan.

Intrinsic (deep) group

The intrinsic back (including dorsal tail) musculature is derived from the myotomes or epaxial portions of the myomeres (dorsal to the lateral line of lower vertebrates), and remains in a relatively undifferentiated condition. The sixth division, comprising the mm. levatores costarum, is placed here for topographic reasons alone, for in reality this is a portion of the external layer of the lateral division of the thoraco-abdominal musculature, being closely related to the external intercostals. The muscles of the tail included within this group are the mm. abductor caudae lateralis, abductor caudae medialis, extensor caudae lateralis, and extensor caudae medialis. Of these, the first three are divisions of the long system, while the last named seems likely to be a part of the transversospinal system.

a. Spino-occipital system

M. SPLENIUS (fig. 40). This is represented only by the splenius capitis, the cervical portion of this sheet being absent. The muscle is extremely heavy, especially along its lateral border. Origin is from the midline between the inion and the fourth thoracic spine, but in some specimens it does not quite attain the former point. Insertion is powerful, along the superior nuchal line of the occipital bone to the mastoid. *Nerve-supply:* Lateral branches of the dorsal rami of the upper nn. cervicales.

b. Long system

This division, frequently termed m. erector or extensor spinae, is longitudinally divisible into a lateral m. iliocostalis and a more medial m. longissimus. In the lumbar region the two are barely separable and are very intimately connected with the lumbodorsal aponeurosis, which is a tough, tendinous sheet beneath the lumbodorsal fascia. This aponeurosis, covering the spinalis, longissimus, and part of the iliocostalis lumborum muscles, arises from the spines of the sacral and lumbar vertebrae, its fasciculi extending in a laterocranial direction. Laterally, in the lumbar region, the lumbodorsal aponeurosis gives way abruptly to the muscular fibers of the m. iliocostalis.

M. ILIOCOSTALIS (fig. 41). This is divisible into two parts, lumbar and dorsal, no cervical portion being present. (1) Iliocostalis lumborum: Caudal to the thorax this is differentiated only in that it is fleshy, as contrasted to the aponeurotic covering of the adjacent m. longissimus. Its fibers accordingly arise from the cranial margin of the ilium and from the lateral border of the longissimus. The more caudal fibers curve around the lateral border of the muscle and insert upon the transverse processes of the lumbar vertebrae. The more superficial of the cranial fibers insert by narrow tendons upon the eleventh to the eighth ribs (circa), while the deeper of the cranial fibers insert broadly and fleshily upon the twelfth rib. (2) Iliocostalis dorsi: This is separable from the pars lumborum only artificially. It occurs as muscle bundles, the more caudal of which take fleshy origin from the last rib upon the lateral margin of the muscle mass. Insertion of the eight (or seven) bundles is by narrow tendons, laterally situated, upon the upper seven (or sometimes six) ribs and the transverse process of the seventh cervical vertebra, the latter bundle having secondary attachment to the first four ribs as well.

M. LONGISSIMUS (fig. 41). This is situated medial to the m. iliocosta-

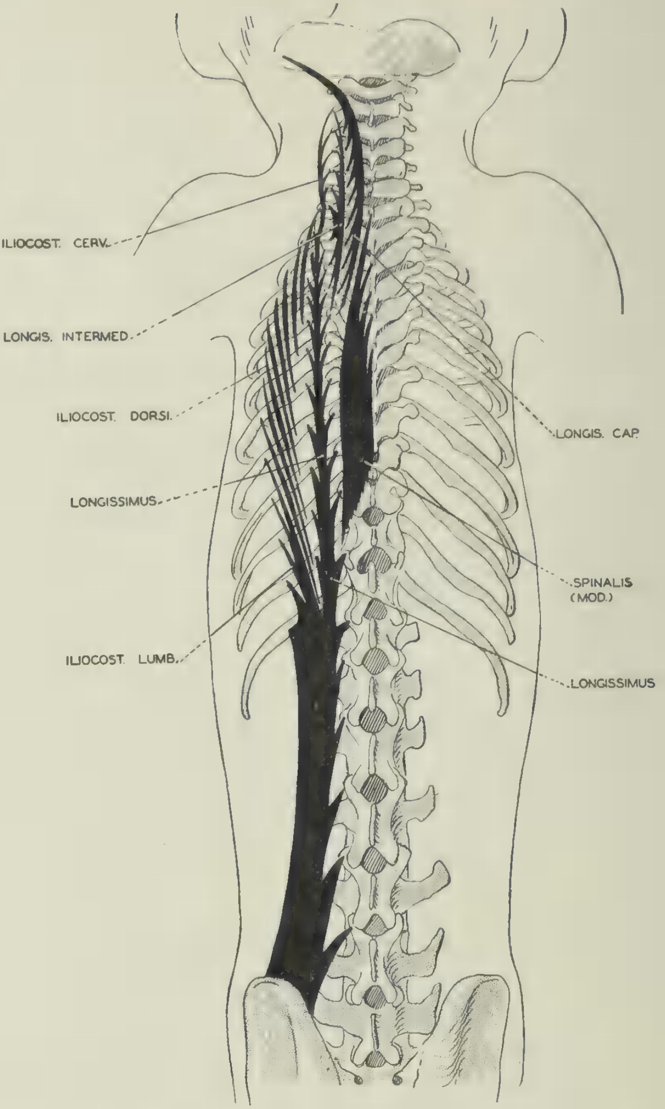

FIG. 41. Semidiagrammatic view of the long system of the intrinsic back muscles.

lis. Three parts can be recognized, a dorsal, a cervical and a capital. (1) Longissimus dorsi: This arises from the medial part of the iliac tuberosity and the deep surface of the lumbodorsal aponeurosis. It gives off fibers which pass medially and cranially to insert upon the lumbar vertebrae, attaching to the bone at the roots of the vertebral arches, chiefly upon the anapophyses, the tendons of the deep medial division of the transversospinal system, and the surrounding periosteum. The fibers which continue cranially take origin chiefly from the deep surface of the lumbodorsal aponeurosis. They insert mostly by tendinous fasciculi upon the anapophyses of the lower thoracic vertebrae. Farther cranialward the anapophyses are but slight prominences dorsal to the tubercular attachment of the ribs, and it is upon these that the fasciculi insert. There is an additional outer series of insertions, largely fleshy, upon each rib close to its tubercle. On the first rib, however, the attachment is single, instead of double as upon the others. In addition to these chief longissimus attachments there are also weaker, secondary attachments of muscle fibers to adjacent structures, such as the tendons of the m. semispinalis. Cranialward the longissimus dorsi extends into the neck, inserting by tendinous fasciculi upon the transverse processes of the lower six cervical vertebrae. This cervical prolongation is dintinct from the longissimus cervicis. (2) Longissimus cervicis: This is located just medial to the cervical portion of the pars dorsi. It is a slender slip arising from the tubercular processes of (usually) the first five thoracic vertebrae and inserting by tendinous fasciculi upon the transverse processes of (usually) the last six cervical vertebrae. (3) Longissimus capitis: This lies medial to the pars cervicis. It arises from the fasciculi of origin of the longissimus cervicis (therefore usually from the first five thoracic vertebrae) and the transverse processes of the last four or five cervical vertebrae. The robust insertion is upon the mastoid process just deep to the lateral border of the m. splenius.

M. EXTENSOR CAUDAE LATERALIS. This is merely a caudal division of the longissimus complex. It arises from the metapophyses of about the second to fifth lumbar vertebrae, the slender muscle mass being situated mostly deep between mm. multifidus and longissimus. Upon the free part of the tail it resolves itself into tendons which pass along the dorsal aspect of the tail to attachments upon the spinous processes and metapophyses of several of the more proximal caudal vertebrae.

M. ABDUCTOR CAUDAE MEDIALIS. This likewise is a caudal division of the m. longissimus. It occupies the space between the lateral abductor and the lateral extensor of the tail. Origin is from the deep surface of the tough aponeurotic investment of the lateral extensor muscle, from the dorsal border of the ilium just below the crest and adjoining the sacrum, and from the dorsal surface of the sacrum. Insertion is upon the base of the transverse processes of the most proximal caudal vertebrae.

M. ABDUCTOR CAUDAE LATERALIS. This also is to be regarded as a caudal division of the m. longissimus. It arises from the transverse processes of the last sacral and the most proximal caudal vertebrae, and inserts upon the lateral processes of the caudal vertebrae.

Nerve-supply: The various divisions of the long system are innervated by lateral branches of the dorsal rami of the nn. spinales.

c. Spinospinal system

M. SPINALIS (fig. 41). This is the most medial division of the superficial portion of the deep back musculature. Its origin is much modified in that it has spread laterally over the deeper musculature. Lumbar, dorsal, and cervical portions are recognizable, although the last division may be absent. (1) Spinalis lumborum, confined to the lumbar region, has its fibers arising from the deep surface of the lumbodorsal aponeurosis close to the spinous processes, instead of from the latter as is more usual in mammals. The rather short fibers extend medially and cranially to attach upon the spinous processes of the lumbar vertebrae. In the region of the first lumbar vertebra the fibers are usually not separable from surrounding muscular tissue. (2) Spinalis dorsi also has its origin modified. It arises, superficial and fleshy, about two centimeters in width, from the superficial surface of the lumbodorsal aponeurosis at a variable point in the lower thoracic region (eighth to eleventh ribs). The fibers extend slightly medially and cranially, to insert upon the tips of the spinous processes of the last cervical and first several (sometimes half or more) thoracic vertebrae. There exists no proof that this division is not a modified semispinalis element, but it is more likely a portion of the spinalis system. (3) Spinalis cervicis may be present in the form of a few fibers extending between (usually) the spinous process of the axis and that of the first thoracic vertebra. *Nerve-supply:* Medial branches of the dorsal rami of the nn. spinales.

d. Transversospinal system

The elements of the deep medial system, consisting of fibers of the mm. semispinalis, multifidus and rotatores, are even more intimately associated and more intricate than in man, so that it is practically impossible to resolve this system into its different components. Muscle fibers in the lumbar region arise from the metapophyses, in common with tendons, from these tendons, and to a lesser extent from the deep surface of the lumbodorsal aponeurosis. The direction of these fibers, which are both muscular and tendinous, is for the most part mediodorsocranial, passing from the lateral processes of the vertebrae to the spines or the occiput, but in addition there are fibers arising from the tendons and extending ventrocranially to attach upon the anapophyses. The heaviest tendons of this division arise solely from the lumbar and last three thoracic vertebrae, usually the only vertebrae having definite metapophyses.

M. SEMISPINALIS. Cranially there appears to be much variability in the extent of the semispinalis elements. They comprise transversospinal fibers bridging more than four vertebral spaces and are indubitably present only in the upper thoracic and cervical regions. The semispinalis capitis is separable into a thinner, superficial, or more medial m. biventer cervicis, and a heavier, shorter, more lateral m. complexus. The former arises from the tubercular processes (metapophysial elements) of several of the upper thoracic vertebrae (third to sixth, or fourth to seventh) and inserts upon the medial quarter or third of the superior nuchal line of the occipital bone. The complexus arises from the tubercular processes of those thoracic vertebrae cranial to the origin of the biventer cervicis and from the transverse processes of the last five or six cervical vertebrae; insertion is upon the medial half or two-thirds of the superior nuchal line just deep to the biventer cervicis. The semispinalis cervicis, lying just deep to the semispinalis capitis, arises by tendon slips from the tubercular processes of the first six or all of the cervical vertebrae. It inserts upon the spinous processes of usually the last six cervical vertebrae, the attachments to the last five being tendinous and weak, and that to the axis chiefly fleshy and very heavy.

M. MULTIFIDUS. These fibers, consisting of those transversospinal elements that bridge from two to four vertebral spaces, occur throughout the entire column, but for the most part they are inseparably fused with the semispinalis, so that they are demonstrable only with difficulty.

MM. ROTATORES LONGI ET BREVES. These are more easily separable, especially cranialward. They are the transversospinal fibers that bridge one vertebra (longi) or attach to the adjoining spinous process (breves).

M. EXTENSOR CAUDAE MEDIALIS. This muscle is the caudal division of the transversospinal system, particularly of the m. multifidus. It arises from the spinous processes of the sacral and proximal caudal vertebrae. In some instances the origin may extend into the lumbar region. Insertion is by tendon upon the metapophyses of the basal caudal vertebrae, rapidly becoming smaller caudalward.

Nerve-supply: The entire transversospinal system receives branches from the dorsal rami of the nn. spinales.

e. Intervertebral system

This may be divided into a modified intertransverse or deep cervico-occipital group (comprising four muscles), an intertransverse group, and an interspinous group. The first of these divisions is particularly well developed in the macaque.

M. OBLIQUUS CAPITIS INFERIOR. Origin is from the spinous process of the axis, the fibers extending laterocranially to insert upon the transverse process of the atlas.

M. OBLIQUUS CAPITIS SUPERIOR. This arises from the tip of the transverse process of the atlas. Its fibers run almost parallel to the vertebral column to their insertion upon the border of the supra-occipital bone.

M. RECTUS CAPITIS POSTERIOR MAJOR. This is particularly well developed, to the extent where it almost covers the m. rectus capitis posterior minor. Origin is from the spinous process of the axis. Insertion is broad, upon almost the entire lateral part of the supra-occipital bone, partly beneath the m. obliquus capitis superior.

M. RECTUS CAPITIS POSTERIOR MINOR. This for the most part lies deep to the preceding muscle. It arises from the mid-dorsal line of the atlas and inserts upon the medial portion of the supra-occipital bone.

Nerve-supply: The four muscles of this group are innervated by branches of the dorsal rami of nn. cervicales I and II.

MM. INTERTRANSVERSARII. These pass between the transverse processes of the vertebrae. They are mostly tendinous, being prominent as fleshy bundles only in the cervical region, where they occur as a relatively heavy muscular element between the transverse processes of the upper three or four cervical vertebrae, the superficial fibers passing over two or three vertebral spaces. In the lower cervical region the fibers pass over but one space. The intertransversarii of the caudal region are extremely variable, as indicated by the variability of the transverse processes of the tail base. In perhaps the most typical form the first of these muscles takes origin from the transverse process of the third caudal vertebra. Some of its deeper fibers insert upon the transverse process of the fourth caudal, but most of them continue to the fifth, passing dorsally around the origin of the next intertransverse bundle. This typically takes origin from the fourth caudal vertebra, and others arise in sequence from succeeding vertebrae, but the subsequent bundles rapidly become weaker. There is considerable variability in attachment in that a bundle may pass over three vertebral spaces instead of two, or the attachment to one of the transverse processes may be lacking. *Nerve-supply:* The dorsal portions of these muscles are believed to be innervated by branches of the dorsal rami, and the lateral portions by branches of the ventral rami of nn. spinales.

Mm. INTERSPINOSI. These muscles, which connect adjoining spinous processes, are for the most part ligamentous, and exhibit few muscle fibers. *Nerve-supply:* Medial (supposedly) branches of the dorsal rami of the nn. spinales.

f. Levatores costarum system

Mm. LEVATORES COSTARUM. These occur as bundles arising from the transverse processes of the last cervical and upper eleven thoracic vertebrae. The fibers of each bundle diverge laterocaudally to insert upon the cranial border of the rib below. The longer element, passing over two costal spaces, such as occurs in man, is absent. *Nerve-supply:* Nn. intercostales and presumably also the ventral ramus of n. cervicalis VIII.

Action. The intrinsic back musculature is constantly in use for maintaining the posture of the head, trunk and tail, and for equilibration. Bilateral action extends the column, and unilateral produces bending to one side and a variety of rotational movements of the column and of the pelvis. As the division of the musculature suggests, the action and interaction is extremely complicated. The two abductor divisions of the tail accomplish dorsolateral movement rather than strict abduction. The levatores costarum expand the ribs.

Comparative anatomy. The intrinsic back muscles are but slightly altered representatives of the segmented myotomes of the lower vertebrates. They form a closely knit complex exhibiting such a degree of variation that it is impossible to determine homologies in all details. The dorsal caudal musculature has experienced enormous reduction in those primates lacking an external tail. In man it is represented solely by the vestigeal and inconstant m. sacrococcygeus posterior (= extensores caudae) and by occasional vestiges of the dorsal abductors.

Muscles of the Upper Extremity

The musculature of the upper extremity may be divided into two main groups, comprising the muscles of the shoulder girdle and those of the extremity proper (upper arm, fore arm, and hand). Both of these groups are innervated solely by branches of the brachial plexus, which is derived from the ventral rami of the lower cervical and upper thoracic nerves (C5–T2). The plexus, in turn, is divisible into dorsal (posterior cord) and ventral (lateral and medial cords) strata. The dorsal division provides the nerve-supply for the entire shoulder girdle musculature and for the dorsal or extensor muscles of the extremity proper; the ventral division innervates the ventral or flexor muscles of the extremity proper (including the pectoral musculature).

MUSCLES OF THE SHOULDER GIRDLE

The scapula is clothed entirely by muscles derived from the dorsal portion of the upper extremity musculature. These thus receive branches from the posterior cord of the brachial plexus. Of the muscles placed within this group, only one, the m. serratus anterior, is connected with the trunk, while the others pass between the scapula and the humerus. The serratus is therefore considered as extrinsic, and the others as intrinsic.

Extrinsic group

M. SERRATUS ANTERIOR (figs. 35, 36, 40, 42). For convenience this muscle may be divided into cervical and thoracic parts, although the two are continuous. The former arises by separate digitations from the transverse processes of the last four to six cervical vertebrae. The thoracic portion likewise arises by pointed digitations from the caudal borders of the first nine or ten ribs, the points of the serrations being about two centimeters dorsal to the beginning of the costal cartilages. Fibers of the cervical portion insert along the medial margin of the vertebral border of the scapula, from the coracovertebral angle to the scapular spine; those of the thoracic part insert, as a continuation of the preceding, from the scapular spine to the glenovertebral angle. At the latter point the fibers from the lower four or five digitations converge to a part of the insertion that is stronger and more tendinous than the rest. *Nerve-supply:* The cervical portion receives a branch of n. dorsalis scapulae in company with twigs from the ventral ramus of n. cervicalis IV; the thoracic part is innervated by n. thoracalis longus.

Action. The more cranial part of the serratus anterior can move the dorsal part of the scapula cranialward or the opposite end caudalward, while the intermediate part moves it in a ventral direction. The muscle is doubtless most frequently used for maintaining the position of the scapula and in conjunction with the trapezius and rhomboideus for fixing the vertebral border of the scapula. It is an important respiratory muscle when the scapula is fixed. In man its function is complicated, action of the lower part being inhibited until the arm has been raised, and a similar condition may well obtain in the macaque.

The *comparative anatomy* of the m. serratus anterior, highly variable in the number of its serrations, has already been discussed (p. 120).

Intrinsic group

✓M. DELTOIDEUS (figs. 35, 36, 40, 42, 43). This is composed of three parts according to origin: A clavicular (cleidodeltoideus), an acromial (acromiodeltoideus), and a spinal (spinodeltoideus). They are not normally separable from each other, however. The clavicular portion arises from the entire clavicle (but not from the capsule of the claviculo-manubrial joint). It exhibits various degrees of fusion with the adjacent fibers of the m. pectoralis major. The acromial portion can be distinguished by the fact that its superficial belly is aponeurotic. Near insertion the fibers of the clavicular and acromial parts decussate with each other. The spinal part arises in a fan-shaped manner from a tough

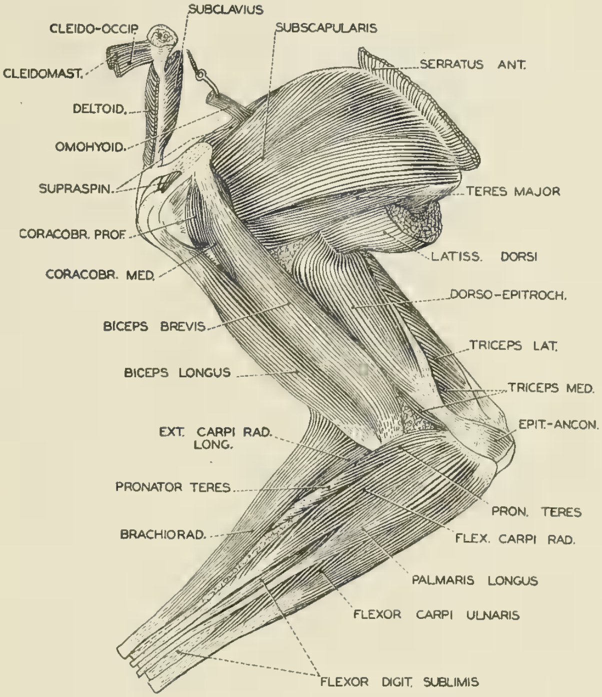

FIG. 42. Muscles of the right scapula, upper arm and forearm, medial view.

aponeurosis attached to the caudal border of the scapular spine, with heavier fasciculi from the dorsal part. The aponeurosis arches over the m. infraspinatus to an attachment upon the glenovertebral angle of the scapula (so that origin of the spinodeltoid is actually from the glenovertebral angle and the spine). The entire muscle inserts upon the lower half of the deltoid crest of the humerus. *Nerve-supply:* N. axillaris.

M. TERES MINOR (fig. 43). This arises from the axillary border of the scapula along an area extending from the expansion of the m. teres major to the scapular neck. Some few fibers may take origin from the surface of the m. infraspinatus. Insertion is chiefly tendinous upon the distal part of the greater tuberosity of the humerus adjoining the insertion of the infraspinatus. *Nerve-supply:* N. axillaris.

M. TERES MAJOR (figs. 40, 42, 43). Origin is from the lateral surface of the expansion of the glenovertebral angle of the scapula and from the surface of the adjoining part of the m. subscapularis. The muscle accompanies the subscapularis for some distance, passing immediately deep (medial) to the long head of the m. triceps. Toward insertion it passes deep to the m. coracobrachialis medius and partly deep (lateral) to the tendon of the m. latissimus dorsi. Here it is joined by a tendon from the dorsal part of the latter muscle and inserts upon the posterior border of the intertubercular sulcus of the humerus just below the surgical neck of the bone. *Nerve-supply:* The lowest of the nn. subscapulares.

M. SUPRASPINATUS (figs. 40, 42, 43). This is a rather intricate muscle. It is composed of three parts: (1) Pars superior is a superficial slip arising from the cranial border of the scapula from about the attachment of the m. omohyoideus to the coracoid process; (2) pars inferior, likewise a superficial slip arising along the cranial border of the scapular spine under cover of the m. atlantoscapularis anterior; and (3) pars proprius, the major portion of the muscle, arising from the entire supraspinous fossa of the scapula. The three parts converge into a common tendon which passes beneath the clavicle and the coracoclavicular ligament to insert upon the highest point of the greater tuberosity of the humerus. *Nerve-supply:* N. suprascapularis.

In addition there at times is present in the macaque a separate division of the m. supraspinatus which may be termed *m. intraspinatus.* It arises from the distal border of the scapular spine between the acromion and the neck, bounding the greater scapular notch, and inserts upon the greater tuberosity of the humerus between the mm. supraspinatus and infraspinatus. *Nerve-supply:* Separate branch of n. suprascapularis.

M. INFRASPINATUS (fig. 43). This arises from all of the infraspinous fossa of the scapula, excepting only that part (occupied by the m. teres major) adjoining the glenovertebral angle. The area of origin includes the caudal surface of the spine, and superficial fibers arise also from the deep surface of the m. deltoideus in this region. Upon the deep surface of the muscle there develops a strong tendon upon which the muscle fibers insert in a pennate manner. This tendon inserts strongly upon the upper part of the posterior border of the greater tuberosity of the humerus. *Nerve-supply:* N. suprascapularis.

M. SUBSCAPULARIS (fig. 42). This is a multipennate muscle arising from the entire medial surface of the scapula. Its fibers converge, passing beneath the common coracoid tendon of the short biceps and coracobrachialis muscle to insertion upon the entire area of the lesser tuberosity of the humerus. *Nerve-supply:* A variable number (five or less) of branches constituting the nn. subscapulares.

Action. In the quadrupedal posture the deltoid is a muscle of prime importance in protraction, retraction, and abduction of the arm. The supraspinatus is used chiefly for fixation of the shoulder joint, a function shared by the infraspinatus, which, with the teres minor, is also a lateral rotator of the humerus. The latter muscle can also retract the arm, as does the teres major. The subscapularis is a medial rotator of the humerus, but its chief function is in fixation of the joint.

Comparative anatomy. The mm. teres minor and deltoideus belong in close association. The latter is only occasionally distinctly separable into its component parts. The cleidodeltoid is particularly well developed in those primates lacking the clavicular origin of the m. pectoralis major. The m. teres major is related phylogenetically to the m. latissimus dorsi and fusion of the two is occasionally encountered in mammals: This is to be regarded as simulating the primitive condition. The remaining muscles of this group seem to vary only within relatively narrow limits.

MUSCLES OF THE UPPER ARM

The muscles of the upper arm are naturally divisible into flexor and extensor components.

Flexor (anterior) group

M. BICEPS BRACHII (figs. 36, 42, 43). This is composed of two distinct heads, a short and a long. The caput breve, in common with the two divisions of the m. coracobrachialis, arises by a tendon from the tip of the coracoid process. At the middle of the upper arm, or a bit beyond, it fuses with the caput longum, the two heads inserting by a common tendon upon the bicipital tuberosity of the radius. The caput longum arises from the supraglenoid tuberosity of the scapula at the lateral base of the coracoid process. The stout tendon pierces the capsule of the shoulder joint and continues down the upper arm lateral to the caput breve, fusing with the latter as stated above. A lacertus fibrosus to the ulnar side of the fore arm fascia is usually absent. *Nerve-supply:* N. musculocutaneus.

M. CORACOBRACHIALIS PROFUNDUS (fig. 42). Origin of this short muscle is from the deep surface of the common coracoid tendon and partly from the coracoid process proper. It passes laterally beneath the short biceps and coracobrachialis medius muscles to insert upon the surgical neck of the humerus just above the tendon of the m. latissimus dorsi, its fibers overlapping the latter structure for a few millimeters in some instances. *Nerve-supply:* A separate branch of n. musculocutaneus.

M. CORACOBRACHIALIS MEDIUS (fig. 42). This arises from the aforementioned common coracoid tendon, deep to the biceps breve, separating from the latter at about the level of the tendon of the m. latissimus dorsi. It inserts, chiefly fleshily, for a distance of some two or three centimeters upon the middle of the medial side of the humeral shaft between the m. brachialis and the medial head of the m. triceps. *Nerve-supply:* N. musculocutaneus.

M. BRACHIALIS (fig. 43). This arises from the shaft of the humerus along an oblique line extending from above the termination of the m. deltoideus upon the lateral side of the upper arm to a point well below the deltoid on the medial side. The lateral origin of the muscle may extend far up the humerus, in extreme instances approaching the surgical neck of the bone. Insertion is upon the ulna in the region of the coronoid process. *Nerve-supply:* N. musculocutaneus or branches of an anastomosis between n. musculocutaneus and n. medianus.

Action. In man, and presumably in the macaque, the biceps brachii is first a supinator of the forearm, after which action it may act strongly as a flexor of that segment. It also assists the coracobrachialis medius (and deltoid) in protraction of the upper arm. The coracobrachialis profundus rotates the upper arm medially. The brachialis is a pure flexor of the forearm.

Comparative anatomy. The two heads of the m. biceps brachii may occasionally be separate for their entire length (normal in *Tarsius*). There may be accessory heads, not rare in man. In mammals the short head is sometimes absent (usually in the Lorisinae), while in gibbons it is normally replaced by a humeral head arising from the lesser tuberosity. Biceps insertion among the lower mammals is variable. It may be upon either radius or ulna or upon both bones. In gibbons the superficial fibers are continuous with those of the fore arm flexors. Among the primates a lacertus fibrosus is normally present in man only.

The m. coracobrachialis is primitively composed of three parts, superficialis, medius and profundus, the first of which is very rare in mammals. Prosimians and monkeys usually have both medius and profundus, but only the former is normally present in anthropoid apes and man. Piercing of the medius by the musculocutaneous nerve is, with occasional exceptions, confined to the anthropoids and man.

The primitive condition of the m. brachialis is two-headed, and this arrangement is present to some degree in practically all species of primates. Occasionally, as in *Tarsius*, the two parts may be entirely separate. Incorporation of some of the fibers of the m. brachioradialis, resulting in dual innervation, may occur; this is very frequent in man.

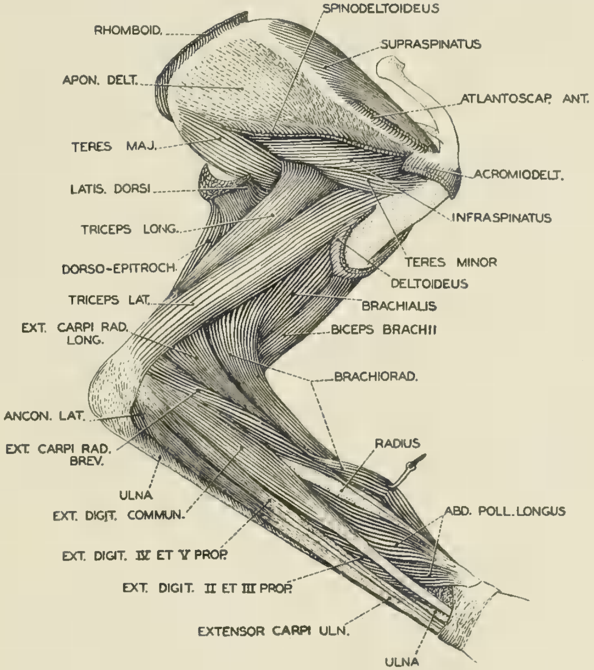

FIG. 43. Muscles of the right scapula, upper arm and forearm, lateral view.

Extensor (posterior) group

M. DORSO-EPITROCHLEARIS (figs. 36, 40, 42, 43). This is really a part of the triceps complex that has become secondarily connected with the m. latissimus dorsi. It arises chiefly fleshily from the muscle belly or tendon of the latissimus some two centimeters before the insertion of the latter. Passing down the medial aspect of the arm it gradually narrows, abruptly developing a tendon in the last quarter of the brachium. From this point an aponeurosis continues distally over the elbow to become attached to the superficial olecranon fascia and the medial epicondyle of the humerus. *Nerve-supply:* Highest branch of n. radialis.

M. TRICEPS BRACHII (figs. 40, 42, 43). This arises by three distinct heads, a long, a lateral, and a medial. The caput longum arises by tendinous fasciculi from the lower half of the axillary border of the scapula, and its relationship to the caput laterale is intricate. Insertion of its fibers is upon the common triceps tendon attached to the tip of the olecranon process of the ulna. The caput laterale arises from the posterolateral surface of the humeral shaft adjoining the insertions of the mm. teres minor and spinodeltoideus. Insertion is upon the common triceps tendon. The caput mediale takes fleshy origin from practically the entire posterior aspect of the shaft of the humerus. Insertion is partly upon the common tendon and partly by fleshy fibers upon the radial border of the olecranon mostly deep to the insertion of the caput laterale. *Nerve-supply:* All three heads of the m. triceps receive branches of n. radialis.

M. ANCONEUS LATERALIS (fig. 43). This is in reality a distal extension of the triceps. It arises from the posterolateral aspect of the capsule of the elbow joint. The fibers spread in a fan-shaped manner to a fleshy insertion along the lateral border of the ulna just below the elbow joint. *Nerve-supply:* N. radialis.

Action. The extensor muscles of the brachium are extensors of the fore arm, and when the arm is extended the long head of the triceps and the dorso-epitrochlearis aid the latissimus dorsi in its recovery.

Comparative anatomy. The triceps complex is rather conservative in mammals, except for the extent of the long head and the definition of the m. dorso-epitrochlearis. The former is usually more extensive in lower primates than in man and may actually cover the glenovertebral angle of the scapula. The m. dorso-epitrochlearis is normally absent in man, but is found in all prosimians and monkeys, and usually in anthropoid apes.

MUSCLES OF THE FORE ARM

These are also divisible into flexor and extensor groups.

Flexor (volar) group

For topographic purposes this may be considered as arranged in four layers:

(1) m. pronator teres
(1) m. flexor carpi radialis
(1) m. palmaris longus
(1) m. flexor carpi ulnaris
(1) m. epitrochleo-anconeus
(2) m. flexor digitorum sublimis
(3) m. flexor digitorum profundus
(4) m. pronator quadratus

M. PRONATOR TERES (fig. 42). This is situated upon the lateral side of the volar surface of the fore arm, adjoining the m. brachioradialis.

It arises chiefly from the ulnar epicondyle of the humerus, but at times from the adjacent joint capsule as well. It is fused for a considerable extent with the mm. flexor carpi radialis and flexor digitorum sublimis. The deep head of human anatomy is lacking. Insertion is by a flat tendon upon the middle third of the lateral and volar surfaces of the radius. *Nerve-supply:* N. medianus.

✓M. FLEXOR CARPI RADIALIS (figs. 42, 44, 45). This muscle lies between the mm. pronator teres and palmaris longus. It arises from the ulnar epicondyle of the humerus and the capsule of the elbow joint. It is fused for a distance with the m. pronator teres and to a lesser extent with the m. flexor digitorum sublimis. Insertion is by a flattened tendon that passes beneath the volar transverse carpal ligament to attachment upon the volar base of the second metacarpal bone, and sometimes upon the third as well. *Nerve-supply:* N. medianus.

✓M. PALMARIS LONGUS (figs. 42, 44). This well developed muscle is the most superficial of the fore arm flexors. It arises from the ulnar epicondyle of the humerus. About midway of the fore arm the muscle fibers give way to a flat tendon that passes superficial to the volar transverse carpal ligament to continue as the palmar aponeurosis. *Nerve-supply:* N. medianus.

✓M. FLEXOR CARPI ULNARIS (figs. 42, 44). It arises from the ulnar epicondyle of the humerus and, chiefly through the medium of a strong aponeurosis, from the lateral aspect of the ulna. Insertion is upon the pisiform bone by a strong tendon that develops only in the lowermost portion of the fore arm. *Nerve-supply:* N. ulnaris.

M. EPITROCHLEO-ANCONEUS (fig. 42). This small muscle, genetically related to the m. flexor carpi ulnaris, is not present in all specimens. Origin is from the medial epicondyloid ridge of the humerus, the fibers passing downward to insert upon the olecranon. *Nerve-supply:* N. ulnaris.

✓M. FLEXOR DIGITORUM SUBLIMIS (figs. 42, 44, 45). This is almost entirely covered by the muscles just described. It arises from the capsule of the elbow joint and the ulnar epicondyle of the humerus, but there is no origin from the coronoid process of the ulna or from the radius. Just beyond the main origin there is given off a deeper head which inserts by a flat tendon into the medial margin of the radial portion of the m. flexor digitorum profundus. The main portion of the muscle gives rise to four tendons. In the middle of the fore arm those tendons which are destined for the second and (especially) fifth fingers lie deep to those for the third and fourth digits, the former tendons in general being continuations of the deeper fibers of the muscle. The tendons pass beneath the volar transverse carpal ligament, through the palm of the hand deep to the palmar aponeurosis, and insert upon the volar surface of the middle phalanges of the second to fifth fingers. *Nerve-supply:* The entire muscle, including the deeper accessory head to the m. flexor digitorum profundus, receives branches of n. medianus.

M. FLEXOR DIGITORUM PROFUNDUS (fig. 45). This is situated between the mm. flexor digitorum sublimis and pronator quadratus. It represents not only the m. flexor digitorum profundus of man, but also the m. flexor pollicis longus of human anatomy. These two parts of the deeper flexor stratum should be considered together, for they are not only simply the ulnar and radial portions, respectively, of the same layer, but a true flexor pollicis longus has not become differentiated from the mass supplying the four more ulnar digits in this monkey. The muscle arises in two portions, radial and ulnar. The former does not precisely correspond to the human flexor pollicis longus, for incorporated with it are the lateral fibers of the human flexor digitorum profundus. The radial portion arises from the medial and volar aspects of the radius and strongly from the interosseous membrane of the fore arm; it also receives an accessory head (as already stated) emanating from the deeper fibers of the m. flexor digitorum sublimis. The ulnar portion takes origin from the lateral and volar aspects of the ulna and slightly from the interosseous membrane. The bellies of the two original portions are distinctly separate from each other. Their tendons, however, fuse somewhat proximal to the wrist. The radial portion produces the whole of the long flexor tendons to the thumb and second finger, and approximately half of the tendon to the third finger. The ulnar segment supplies the remainder of the tendon to the third finger, and the whole of those to the fourth and fifth fingers. In some instances the thumb tendon may be derived in part from the ulnar portion of the muscle. This tendon is always smaller than those passing to the other digits. It does not arise from the radial side of the muscle, but from the middle portion, crossing the tendon to the second finger (and at times that to the third also) volarward in its course to the pollex. There is usually a definite cleavage plane between the portions of the muscle supplying the fourth and fifth fingers. The tendons of the muscle pass beneath the volar transverse carpal ligament deep to the m. flexor digitorum sublimis. Piercing the corresponding tendons of the latter muscle, the four ulnar tendons insert upon the volar aspects of the terminal phalanges of the second to fifth fingers respectively. The pollical tendon inserts upon the volar surface of the terminal phalanx of the thumb. The usual distribution of the tendons emanating from the two portions of the muscle is given in condensed form below:

Radial segment supplies tendons to digits 1 2 3
Ulnar segment supplies tendons to digits 3 4 5

Nerve-supply: The two portions receive branches of n. medianus which come from both the main trunk and volar interosseous division. The muscle normally receives no branch from n. ulnaris as it does in man.

M. PRONATOR QUADRATUS (fig. 45). This muscle lies deep to the m. flexor digitorum profundus and adjoining the interosseous membrane. It occupies only the distal quarter of the fore arm. Origin is from the volar surface of approximately the distal quarter of the shaft of the ulna. The fibers pass radially and distally to insert upon the corresponding portion of the volar surface of the radius. The muscle extends almost to the ends of the fore arm bones. It may exhibit partial division into two layers. *Nerve-supply:* Volar interosseous division of n. medianus.

Action. The pronator teres acts as a flexor of the fore arm when the bones of this segment are fixed to prevent pronation, and otherwise, with the pronator quadratus, accomplishes strong pronation. The palmaris longus first tenses the palmar aponeurosis and in subsequent action then assists the flexores carpi radialis and ulnaris to flex the wrist. In man progressively stronger action of the flexor digitorum sublimis first flexes the second phalanges, and then finally the wrist, while similar action of the flexor digitorum profundus first affects the third phalanges, next the second, and finally the wrist, but apparently neither division affects the first phalanges except indirectly. The muscles of this group, with the exception of the pronator teres, are of but little help in movements of the fore arm upon the upper arm. The action in the macaque may be presumed to be the same except that it apparently has less than the human ability to indulge in complicated movements of a single digit.

Comparative anatomy. The primitive plan of the flexors of the fore arm includes a radial and an ulnar component, a common flexor sheet with superficial (sublimis) and deep (profundus) fibers, all with general origin from the ulnar epicondyle of the humerus, and a pronator element passing from the ulna to the radius. The first two of these, comprising the mm. flexor carpi radialis and flexor carpi ulnaris, are uniformly conservative. The flexor sheet in placental mammals has to all intents separated for its entire length into two parts, and from the superficial component there again has differentiated a palmaris longus element. The middle of the pronator sheet has disappeared, leaving proximally the deep head of the m. pronator teres (but only in some forms), and a distal m. pronator quadratus.

In the anthropoid apes the m. flexor carpi radialis arises not only from the humerus, but from the radius as well; such radial origin occurs as a variant in man.

The m. epitrochleo-anconeus occurs in many mammals. It is found in most lower primates, but only occasionally in the great apes and man. It is apparently a vestige of the primitive humeral origin of the m. flexor carpi ulnaris.

The humeral head of the m. pronator teres is not a part of the primitive pronator sheet, but is a portion of either the original common flexor complex or the radial flexor. An ulnar (or deep) head is encountered in neither prosimians nor monkeys, but is frequent in gibbons and gorillas and is the rule in the other anthropoid apes and man. It is normally absent in other mammals.

There is a tendency for the disappearance of the m. palmaris longus in the higher primates, culminating in the gorilla; this is an extremely variable muscle.

A coronoid origin of the m. flexor digitorum sublimis is usually not encountered among the lower primates, but commonly occurs in man and the chimpanzee. A radial origin of the sublimis occurs among primates only in the anthropoid apes and man.

Complete differentiation of a separate flexor pollicis longus element from the flexor digitorum profundus layer occurs only in man. The tendon to the pollex is greatly reduced or absent in most gorillas and orang-utans, and in a large percentage of chimpanzees; it is normally present in other primates. An accessory head of the deep flexor arising from the sublimis is the rule in lower primates and is not infrequent in man; this represents a primitive connection between the superficial and deep strata of the common flexor sheet.

The m. pronator quadratus is usually present in a relatively undifferentiated condition. Its chief variations relate to the degree of its development.

Extensor (dorsal) group

These muscles may be divided into two strata, a superficial and a deep. To the former belong the first seven muscles described below, and to the deeper layer the remaining five.

M. BRACHIORADIALIS (figs. 42–46). This, the most proximal of the fore arm muscles, originates from the lateral epicondyloid ridge of the humerus and the adjoining intermuscular septum, extending almost as high as the m. deltoideus. The proximal portion is very broad and the flat tendon of insertion is attached to the distal part of the shaft of the radius. The radial nerve passes either medial to the origin of the muscle or pierces it.

M. EXTENSOR CARPI RADIALIS LONGUS (figs. 42, 43, 46). Origin is from the lateral border of the humerus for some two centimeters distal to that of the preceding muscle, and at times also from the radial epicondyle. The tendon passes through the second compartment beneath the dorsal transverse carpal ligament to its insertion upon the dorsal surface of the base of the second metacarpal bone.

M. EXTENSOR CARPI RADIALIS BREVIS (figs. 43, 46). This arises from the upper part of the radial epicondyle of the humerus, adjoining, but distinct from, the origin of the preceding muscle. The tendon passes through the second compartment beneath the dorsal transverse carpal ligament and inserts upon the dorsal aspect of the base of the third metacarpal bone.

M. EXTENSOR DIGITORUM COMMUNIS (figs. 43, 46). It arises from the radial epicondyle of the humerus just below and partly fused with the m. extensor carpi radialis brevis. The tendon passes beneath the dorsal transverse carpal ligament, lying in the third compartment, and splits into divisions for the four radial digits. The terminal tendons are intimately united as far as the heads of the metatarsal bones. They do not insert quite as in man, for there is a broadening of each and attachment along the sides of the basal phalanx, and a further broadening with attachment to the base of the middle phalanx, but no marked continuation to the terminal phalanx.

M. EXTENSOR DIGITI QUARTI PROPRIUS (figs 43, 46). Origin is from the radial epicondyle of the humerus in common with the m. extensor digiti quinti proprius. At a variable situation in the fore arm, or even over the wrist, their common tendon divides into two parts, which pass through the fourth compartment beneath the dorsal transverse carpal ligament. The tendon of the extensor quarti inserts upon the ulnar side of the dorsum of the fourth finger, having attachment chiefly to the basal phalanx.

M. EXTENSOR DIGITI QUINTI PROPRIUS (figs. 43, 46). This arises in common with the preceding muscle, accompanying it as described above, through the fourth compartment beneath the dorsal transverse carpal ligament. Insertion is upon the ulnar side of the dorsum of the fifth finger, chiefly upon the middle phalanx.

M. EXTENSOR CARPI ULNARIS (figs. 43, 46). This muscle, the most ulnar of the fore arm extensors, arises from the radial epicondyle of the humerus. It extends superficially down the fore arm, through the fifth compartment under the dorsal transverse carpal ligament, and inserts upon the dorsal aspect of the base of the fifth metacarpal bone.

M. SUPINATOR. It arises by a strong, broad tendon from the radial epicondyle of the humerus deep to the origin of the mm. extensores digitorum quarti et quinti proprii, and fleshily from the lateral border of the ulna for a distance of about one centimeter. Insertion is upon the proximal half of the radial shaft on its dorsal, lateral and volar aspects, the fibers extending in an oblique direction radialward. It is pierced by the ramus profundus of the radial nerve.

M. ABDUCTOR POLLICIS LONGUS (figs. 43, 46). This, the deepest of the fore arm extensors, arises from most of the lateral border of the ulna, the proximal two-thirds of the dorsal border of the radius, and the interosseous membrane. The fibers rapidly converge as they approach the lateral side of the distal portion of the radius and pass through the first dorsal compartment (not covered by the main dorsal transverse carpal ligament). Insertion is partly upon the radial side of the base of the first metacarpal bone and partly upon the adjacent radial sesamoid. In the lower part of the fore arm the muscle and its tendon may split completely into two separate portions, one of which inserts upon the metacarpal, the other upon the sesamoid bone.

M. extensor pollicis brevis is absent.

M. EXTENSOR POLLICIS LONGUS (fig. 46). This is a relatively weak muscle that arises deep to the m. extensor digitorum communis, from the proximal two-fifths of the lateral part of the dorsal surface of the ulna in proximal continuation of the mm. extensores digitorum secundi et tertii proprii. It passes through the third compartment beneath the dorsal transverse carpal ligament and then diverges laterally, inserting chiefly upon the dorsal surface of the terminal phalanx of the thumb.

M. EXTENSOR DIGITI SECUNDI PROPRIUS (figs. 43, 46). It has a slender origin in common with the m. extensor digiti tertii proprius from the lateral border of the third and fourth fifths of the ulna in distal continuation of the long extensor of the thumb. Somewhat above the wrist the tendon of the extensor secundi splits from the radial border of the muscle, the remainder becoming the extensor tertii. The two tendons pass through the third compartment under the dorsal transverse carpal ligament. Insertion of the extensor secundi is upon the ulnar side of the dorsum of the second finger, with chief attachment upon the basal phalanx.

M. EXTENSOR DIGITI TERTII PROPRIUS (figs. 43, 46). This arises with the preceding muscle, as described above. Its tendon passes through the third compartment under the dorsal transverse carpal ligament and inserts upon the ulnar side of the dorsum of the third finger, with chief attachment upon the basal phalanx.

Nerve-supply: All of the twelve muscles comprising the extensor group of the fore arm receive branches of n. radialis.

Action. The brachioradialis, although one of the extensor group of muscles, is an exceedingly powerful flexor of the fore arm but plays no part in extension of that segment. The remainder of this group are of but slight aid in movements of the fore arm upon the upper arm. Simple extension of the wrist is accomplished by the extensores carpi radialis longus and brevis, and ulnaris, brought into play mostly for fixation, but extension of the wrist is also frequently produced by a very complicated interaction of both flexors and extensors of the digits. Adduction of the hand (radialward) is accomplished by the two extensores carpi radiales, abductor pollicis longus and to a lesser extent the extensor digiti secundi proprius, all assisted by the flexor carpi ulnaris. The supinator accomplishes pure supination. Action by the long extensors of the digits extends only the first phalanges and then the wrist, unless synergists are brought into play, when fixation of the first phalanges is followed by full extension of the digits. The above statements apply to man, but may be presumed to reflect the conditions in the macaque, although to a more moderate degree.

Comparative anatomy. As with the fore arm flexors the primitive plan of the extensor aspect consists of a radial and an ulnar component, a common extensor sheet with superficial and deep divisions, all ideally originating from the radial epicondyle of the humerus, and a supinator element passing from ulna to radius. In the general scheme elaborated from this plan in the placental mammals the original radial extensor has become differentiated into four parts (mm. brachioradialis, extensores carpi radialis longus et brevis, and abductor pollicis longus), whereas the ulnar extensor has remained undivided. The common extensor sheet has split into two layers,—a superficial stratum (m. extensor digitorum communis) to the four ulnar digits, and a deep stratum (mm. extensor pollicis longus and extensores proprii of digits II–V) to all five digits (although the extensores proprii of IV and V have secondarily become superficial in the forearm). The m. supinator is generally simple.

The m. brachioradialis varies in the height of its origin, but as a rule this is lower in man than in other primates. In prosimians, monkeys and man insertion is upon the distal end of the radius, but in some great apes the radial attachment is more proximal, and in gibbons it inserts barely beyond the middle of that bone. The muscle belly may exhibit connections with the m. brachialis.

The mm. extensores carpi radialis longus et brevis normally insert respectively upon the second and third metacarpals in all primates, but additional attachments to the adjacent metacarpals are not infrequent. An accessory insertion of the longus upon the pollical metacarpal occurs commonly in gibbons. The two radial extensors are represented by a single muscle in some mammals, and differentiation into long and short components is a progressive feature. Fusion of their muscle bellies occasionally occurs in man.

The m. extensor carpi ulnaris may send an accessory tendon to the basal phalanx of the fifth finger.

Among the primates the m. abductor pollicis longus may be more or less divided into carpal and metacarpal portions. Its derivative, the m. extensor pollicis brevis, occurs only in higher primates (normally in man and not infrequently in the gorilla).

The variations of the m. extensor digitorum communis are related chiefly to the manner and degree of the connections between the several tendons, and to the deficiency or increase in the normal number of slips. That to the second finger may be isolated. One or more digital tendons, especially those to the second and fifth fingers, may be lacking.

The full complement of deep extensors is present in most prosimians, monkeys, gibbons and orang-utans. In the chimpanzee, gorilla and man this layer is normally reduced to the portions supplying the first, second and fifth fingers, although the tendons of the third and fourth digits occur not infrequently in chimpanzees, and occasionally in the others. The pollical tendon is much stronger in man than it is in the great apes. It may be split into two or more parts, and may also exhibit connections with neighboring muscles.

The m. supinator is subject to relatively slight variation.

MUSCLES OF THE HAND

The hand normally exhibits no intrinsic muscles of the extensor or dorsal group. Its musculature is as follows.

Flexor (volar) group

The *aponeurosis palmaris* (fig. 44) is the volar continuation of the tendon of the m. palmaris longus. It covers the volar muscles and extends toward the distal end of the metacarpus. It is weaker along the borders of the palm. Lesser slips attach themselves to deeper volar structures.

M. PALMARIS BREVIS (fig. 44). This is a small strap-shaped or triangular, subcutaneous muscle. It arises from the ulnar border of the palmar aponeurosis and inserts not only upon the skin of the ulnar border of the hand, but also upon the pisiform bone and the fascia for a few millimeters distalward. *Nerve-supply:* Ramus volaris manus superficialis n. ulnaris.

M. ABDUCTOR POLLICIS BREVIS (figs. 44, 45). This arises from the volar transverse carpal ligament, naviculare and radial sesamoid. The muscle fibers converge to a narrow, tendinous insertion upon the radial side of the base of the first phalanx of the thumb. *Nerve-supply:* N. medianus.

M. OPPONENS POLLICIS (fig. 45). Origin is from the volar transverse carpal ligament, multangulum majus and radial sesamoid. It inserts fleshily all along the radial border of the first metacarpal bone as far forward as its head. The muscle is covered by the m. abductor pollicis brevis and slightly by the superficial head of the m. flexor pollicis brevis. *Nerve-supply:* N. medianus.

M. FLEXOR POLLICIS BREVIS (figs. 44, 45). This is a bicipital muscle. Its superficial head arises from the volar transverse carpal ligament together with the short abductor of the thumb. The muscle splits into two parts, one of which joins and inserts with the m. abductor pollicis brevis, the other inserting ulnarward upon the base of the first phalanx of the thumb. The strong deep head arises from the multangulum minus and base of the second metacarpal bone and splits into two parts, the larger and more superficial of which attaches to the base of the first pollical phalanx on the radial side of the long flexor tendon of the thumb, the smaller and deeper part inserting with the m. adductor pollicis upon the ulnar side of the base of the first pollical phalanx. The deeper part of the deep head is also partly fused at origin with the proximal fibers of the adductor pollicis. *Nerve-supply:* The superficial head is innervated by n. medianus, the deep head is apparently supplied solely by ramus volaris manus profundus n. ulnaris in some specimens and by n. medianus in others.

M. ADDUCTOR POLLICIS (figs. 44–46). This fan-shaped muscle arises from the bases of the second and third metacarpal bones, from the radial side of the central tendon of the contrahentes muscles, and from the second and third metacarpophalangeal joint capsules. The fibers converge to an insertion upon the ulnar side of the base of the first phalanx of the thumb, and usually also by a narrow fleshy extension upon the ulnar side of the second pollical phalanx. *Nerve-supply:* Ramus volaris manus profundus n. ulnaris.

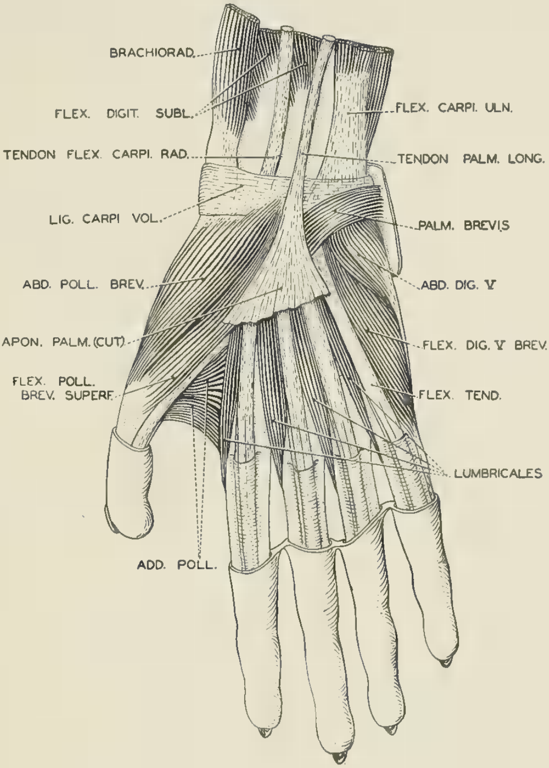

Fig. 44. The more superficial muscles of the right hand, volar view.

M. ABDUCTOR DIGITI QUINTI MANUS (figs. 44, 45). This muscle arises by two heads. The larger has origin from the pisiform bone and volar transverse carpal ligament, and along the ulnar border of the hand from the volar extension of the dorsal transverse carpal ligament. The smaller and more radial head arises together with the m. flexor digiti quinti brevis from the volar transverse carpal ligament. The larger head gives rise to a well developed tendon to which the muscular fibers of the smaller head shortly attach, and which inserts upon the ulnar side of the base of the first phalanx of the fifth finger and the fifth metacarpophalangeal joint capsule. *Nerve-supply:* Ramus volaris manus profundus n. ulnaris.

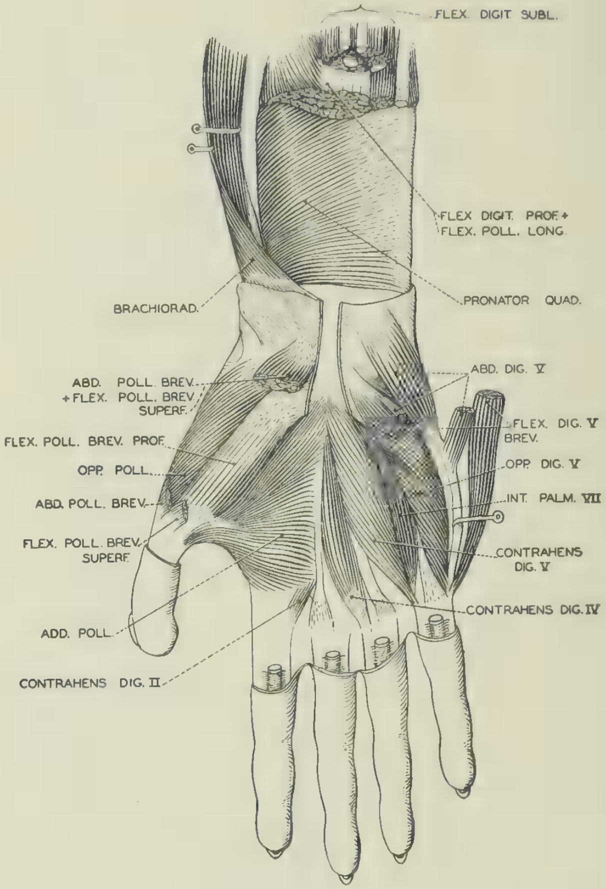

Fig. 45. The deeper muscles of the right hand, volar view.

M. FLEXOR DIGITI QUINTI BREVIS MANUS (figs. 44, 45). Origin is from the volar transverse carpal ligament in common with the smaller head of the m. abductor digiti quinti. Insertion is upon the ulnar side of the basal phalanx of the fifth finger, with an extension to the dorsal surface of the digit. *Nerve-supply:* Ramus volaris manus profundus n. ulnaris.

M. OPPONENS DIGITI QUINTI MANUS (fig. 45). This fleshy muscle lies deep to the preceding. It arises from the volar transverse carpal ligament and hamatum, and inserts with fleshy fibers along the ulnar border of the fifth metacarpal bone for most of its extent. *Nerve-supply:* Ramus volaris manus profundus n. ulnaris.

MM. LUMBRICALES MANUS (fig. 44). These are four in number. They arise in the palm by two heads from the adjacent surfaces of the tendons of the m. flexor digitorum profundus, the most radial lumbrical excepted; this muscle has origin from only the radial side of the deep flexor tendon of the second finger. The insertions are upon the radial sides of the basal phalanges of the second to fifth fingers, respectively, and by definite dorsal extensions into the corresponding extensor aponeuroses. *Nerve-supply:* The two more radial muscles are usually supplied by branches of n. medianus, the two more ulnar usually by branches of ramus volaris manus profundus n. ulnaris.

MM. CONTRAHENTES DIGITORUM MANUS (fig. 45). These are three muscles whose fibers arise from a tendon attached proximally to the bases of the second and third metacarpal bones and the multangulum minus and capitatum. This tendon is continued forward for the length of the third metacarpal bone to its head, and also as a narrow tendon obliquely forward to the head of the fourth metacarpal. The large contrahens of the fifth finger arises by two heads,—one from near the beginning of the contrahens tendon and the other from the ulnar side of its prolongation to metacarpale IV. It inserts upon the radial side of the basal phalanx of the fifth finger. The contrahens of the fourth finger is also a large muscle. Its single head arises from near the beginning of the contrahens tendon and forward from along the ulnar side of its prolongation to the head of metacarpale III; insertion is upon the radial side of the basal phalanx of the fourth finger. The contrahens of the second finger is usually a much smaller muscle, almost completely covered by the m. abductor pollicis. Its fibers take origin from the radial side of the aforementioned tendon running along metacarpale III, and it inserts upon the ulnar side of the basal phalanx of the second finger. The contrahentes are derived from the same muscle sheet as the m. adductor pollicis. The latter is actually the contrahens of the pollex. *Nerve-supply:* The three contrahentes are innervated by branches of ramus volaris manus profundus n. ulnaris, which passes between them and the interosseous muscles.

MM. INTEROSSEI MANUS (figs. 45, 46). These muscles are somewhat variable in their arrangement. In their most complete expression they consist of eleven discrete fleshy slips lying dorsal to the deep volar branch of the ulnar nerve, which separates them from the mm. contrahentes. They arise from the bases of the four ulnar metacarpal bones and the adjacent carpal ligaments. Seven of these slips are the palmar (or volar) interossei, one for each side of the second, third and fourth fingers, and the seventh for the radial side of the fifth digit. The remaining four muscles (the dorsal interossei) take a more dorsal course, passing respectively to the radial side of the second finger, to the radial and ulnar sides of the third finger, and to the ulnar side of the fourth finger. These four muscles can be seen occupying the interosseous spaces dorsally. They are the only interossei that can be seen from the dorsum of the hand.

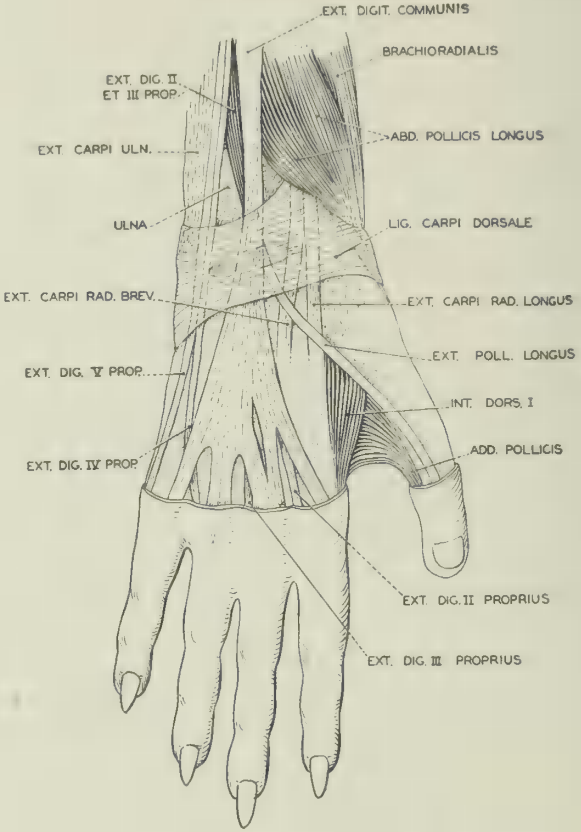

Fig. 46. Tendons of the dorsum of the right hand.

Each interosseous muscle inserts into the side of the basal phalanx of its respective finger, and sends a prolongation to the dorsum of the digit. The four dorsal interossei and the second, fifth and seventh plantar interossei may have partial origin from the plantar surfaces of the shaft of the metacarpal bones on which they lie, but such connections are usually weakly fibrous. In addition, the dorsal interossei may exhibit second and more dorsal heads of origin from the shafts of the adjacent metacarpal bones, but these attachments likewise are usually weak. The first, third, fourth and sixth palmars are really only the volar portions of the four dorsal interossei that are separate from the rest of the muscle. This separation is not clearly apparent in all instances, so that one or more of the palmar set may sometimes be missing. The main origins of the muscles seem to be quite variable. Thus the fifth metacarpal bone may not give rise to interosseous fibers, or the muscles may be more or less segregated into two groups,—a radial set arising chiefly from the second metacarpal bone and carpal ligaments, and an ulnar set arising chiefly from the fourth (and fifth) metacarpal bone and carpal ligaments. In the latter condition the third metacarpal bone is practically devoid of original interosseous fibers. Such segregation of the muscles into two distinct groups is unusual, however, and by no means as marked as in the foot. The arrangement of the dorsal set is, as in man, with respect to an axis passing through the third finger. *Nerve-supply:* All of the interosseous muscles, both palmar and dorsal, are innervated by branches of ramus volaris manus profundus n. ulnaris.

Action. The muscles of the hand function in a very complicated manner, and there is great difficulty in segregating their individual actions. The palmaris brevis draws the hypothenar skin toward the palm. The dorsal interossei effect abduction of the second, third and fourth digits from an axis through the third finger, while the palmar interossei aid the contrahentes digitorum in antagonistic adduction (the fifth finger inclusive). Both sets of interossei, together with the contrahentes, the lumbricales, and the flexor digiti quinti brevis, flex the first phalanges. The lumbricales and interossei likewise take part in extension of the fingers, but apparently affect only the more distal segments. The abductors of the pollex and fifth finger accomplish abduction of their respective digits from the midline of the hand. The opponens pollicis rotates the metacarpal bone of the thumb longitudinally toward the palm (although more weakly than in man), while the opponens digiti quinti similarly affects the fifth metacarpal, although to a lesser degree because of the character of the fifth carpometacarpal joint. As a member of the contrahentes group of muscles the adductor pollicis draws the thumb toward the midline of the hand, and also aids the opponens pollicis in the act of pollical opposition. The flexor pollicis brevis flexes the first phalanx of the thumb; in this action it is probably complemented by the short pollical abductor, adductor and opponens.

Comparative anatomy. The m. palmaris brevis varies in its degree of development. It is absent in some prosimians, usually present in monkeys, absent or weakly developed in gibbons, and lacking in the great apes not infrequently and in man occasionally. A corresponding radial subcutaneous muscle is present in some primates.

The short muscles of the thumb and little finger are subject to minor variations that are chiefly of specialized interest. The m. opponens pollicis, which is a derivative of the m. flexor pollicis brevis, is normally present in all primates. In some individuals, however, it may be poorly developed or lacking. It is generally weaker in the great apes than it is in man.

The mm. lumbricales are exceedingly variable. One or more may be doubled or missing, they may give rise to accessory fasciculi, and others than that of the second finger may arise from only one deep flexor tendon.

The mm. contrahentes digitorum are closely related to the mm. interossei, but the two groups are well differentiated in all mammals. The contrahentes group primitively consists of four muscles passing respectively to the first (m. adductor pollicis), second, fourth and fifth digits, adducting these digits to an axis through the third finger. In some prosimians and monkeys the full complement is present, but in many specimens the elements to the second and fifth fingers are reduced or absent. The contrahentes of fingers II, IV and V are at best but poorly developed in gibbons, only those to IV and V present but reduced in most chimpanzees, while all three are normally lacking in orang-utan, gorilla and man. The m. adductor pollicis is normally present and well developed in all primates.

The mm. interossei are homologous with the mm. flexores breves profundi of lower vertebrates. In all primates there are four dorsal interossei, while the palmar group numbers seven (or six), save in man, where they are reduced to three by the incorporation of four of them with the dorsal interossei. In some prosimians and in all monkeys, gibbons, great apes, and man the dorsals are oriented with reference to an axis through the third finger, this constituting the primitive condition. Those prosimians that depart from this arrangement have the muscles arranged about the fourth digit. The axis very rarely may be through the second finger in man.

Muscles of the Lower Extremity

The musculature of the lower extremity is composed of two main groups, comprising the muscles of the hip and the muscles of the extremity proper (thigh, leg and foot). The elements of both of these groups receive their innervation from the ventral rami of the lumbar and sacral nerves that form the lumbosacral plexus. This plexus, in turn, exhibits two main divisions, ventral and dorsal, but these are less sharply differentiated than in the brachial plexus. The nerves of the ventral division supply a part of the hip musculature, the flexors and adductors of the thigh, the flexor group of the leg, and the plantar musculature of the foot. Branches from the dorsal division innervate a portion of the hip musculature, the extensor groups of thigh and leg, and the dorsal musculature of the foot. It should be noted that whereas the intrinsic musculature of the shoulder girdle is composed entirely of dorsal extremity components, that of the hip girdle belongs to both dorsal and ventral extremity groups.

MUSCLES OF THE HIP

Iliopsoas group

M. PSOAS MAJOR (fig. 48). Origin is from the bodies of the seven lumbar vertebrae and from a variable number of the lumbar transverse processes. In the pelvis it joins the m. iliacus. *Nerve-supply:* Short deep branches of the ventral rami of nn. lumbales I-III and branches of n. femoralis.

M. ILIACUS (fig. 48). This muscle arises from the ventral aspect of the ilium between its acetabular and pubic borders and from the crest downward to the lower margin of the sacro-iliac articulation. Its fibers are joined by those of the m. psoas major, the compound muscle passing over the pelvic brim to a single insertion between the mm. pectineus and quadratus femoris upon the lesser trochanter of the femur. *Nerve-supply:* Branches of n. femoralis.

M. PSOAS MINOR (fig. 48). Origin is from the bodies of (usually) the four upper lumbar vertebrae. The broad, flat, glistening tendon passes downward over the ventral and medial aspects of the m. psoas major to insertion upon the border of the pelvis in the region of the iliopubic junction just ventral to the cranial border of the acetabulum. *Nerve-supply:* Short deep branches of the ventral rami of the upper nn. lumbales.

Action. The psoas minor flexes the pelvis upon the trunk or vice versa. The psoas major and the iliacus act together in strong protraction and lateral rotation of the thigh; when the thigh is fixed they flex the pelvis and lumbar spine and draw them lateralward.

Comparative anatomy. The number of vertebrae involved in the attachment of the mm. psoas major and minor is subject to some variation, as is the degree to which the former may fuse with the m. iliacus. The association of the m. psoas minor with this group is possibly not fundamental. Often it is absent in man and occasionally in chimpanzees and gorillas, but it appears to be uniformly present in other mammals.

Gluteal group

The *fascia lata* (fig. 47), as here defined, is composed of elements chiefly of the so-called iliotibial tract of man. Laterally it is a continuation of the dorsal fascia, and medially it may be considered as a continuation of the m. tensor fasciae latae. It covers the quadriceps femoris group of muscles in a glistening sheet, and between that complex and the m. biceps femoris it is attached to the shaft of the femur. The distal anchorage is upon the superficial structures of the patella and the upper part of the leg.

M. GLUTEUS MAXIMUS (fig. 47). This arises fleshily from the transverse processes of the upper two or more caudal vertebrae, and from the dorsal fascia over the sacrum. Some of the fibers insert directly upon the fascia lata, the remainder converging beneath the cranial margin of the m. biceps femoris to insert by strong tendon bundles upon the greater tuberosity of the femur and along the linea aspera for a distance of a few centimeters. The muscle is fused anteriorly with the m. tensor fasciae latae. *Nerve-supply:* N. gluteus inferior.

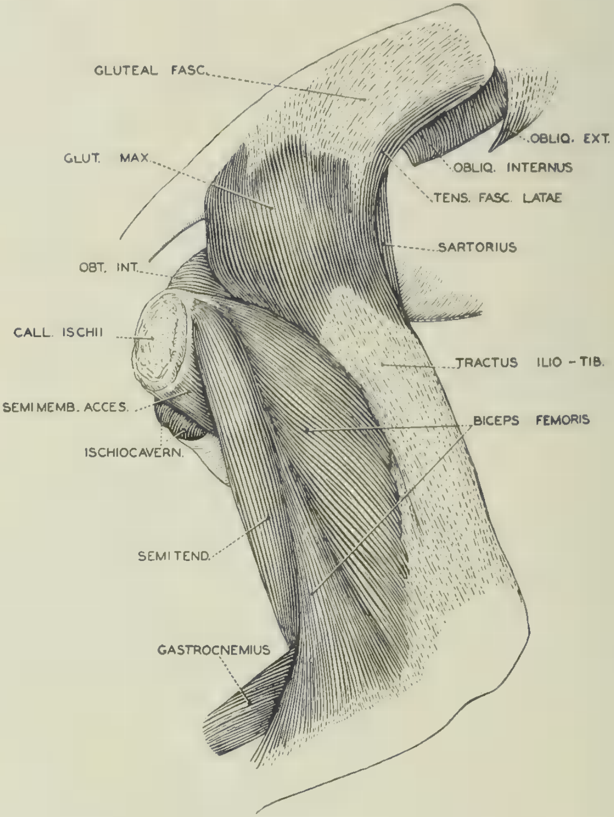

Fig. 47. Muscles of the right hip and thigh, lateral view.

M. TENSOR FASCIAE LATAE (figs. 47, 48). This muscle arises from that part of the fascia coming from the anterior superior iliac spine, and from the acetabular border of the ilium between the mm. gluteus medius and sartorius. The muscle fibers disappear in the fascia lata at about the middle third of the thigh. The upper part of the muscle is fused with the m. gluteus maximus. *Nerve-supply:* N. gluteus superior.

M. GLUTEUS MEDIUS. This muscle, which is much thicker than the m. gluteus maximus, is covered by the latter and by the m. tensor fasciae latae. It occupies most of the gluteal fossa of the ilium. Origin is from the deep surface of the dorsal fascial, from the superficial surface of the deep fascia over the sacrum, from the dorsal border of the ilium, and from the acetabular border of this bone where it is fused with the origin of the m. tensor fasciae latae. The fibers converge to a strong insertion upon the tip of the great trochanter of the femur, at this point fusing with the insertion of the m. piriformis. *Nerve-supply:* N. gluteus superior.

M. PIRIFORMIS. This is a very robust muscle. It is quite distinct, except at insertion, where it fuses with the deep fibers of the m. gluteus medius. Origin is from the transverse processes of the last two sacral vertebrae. It passes immediately superficial to the n. ischiadicus to insert upon the medial tip of the great trochanter. *Nerve-supply:* Branch of n. lumbalis VII (n. piriformis).

M. GLUTEUS MINIMUS. This lies beneath the m. gluteus medius. Origin is from the caudal half of the ilium, chiefly from the dorsal border, and also partly from the fasciculi of the m. ischiocaudalis. The fibers converge to a strong insertion upon the cranial border of the great trochanter of the femur. The more ventral fibers may be practically segregated to form a separate, stout division (frequently termed m. scansorius) until near insertion. *Nerve-supply:* N. gluteus superior.

Action. The actions of the gluteal musculature are quite complex and difficult to analyze. All of the group probably take part in strong retraction of the thigh in the quadrupedal posture, and in addition are major abductors. The tensor fasciae latae and gluteus maximus tighten the fascia lata.

Comparative anatomy. The gluteal group in mammals exhibits various degres of differentiation. Three main divisions (maximus, medius, and minimus) are generally recognizable. Gluteus maximus fibers (not infrequently separate from the main portion of the muscle) passing from tail base to femur are sometimes designated m. caudofemoralis, femorococcygeus, or agitator caudae. An iliac origin of the m. gluteus maximus is generally lacking in lower mammals. The m. tensor fasciae latae is variable in development or at times is absent (as is commonly the case in prosimians). In most lower primates it is less well developed than it is in man, and is usually but poorly separated from the adjoining m. gluteus maximus. In the orang-utan the muscle is either absent or greatly reduced, but in the other anthropoids it is generally present and frequently distinct from the m. gluteus maximus. The m. piriformis at times may not be differentiated as a distinct structure, being fused with the m. gluteus medius; this is not infrequent in monkeys. From the deeper part of the gluteal sheet there may be derived a division termed m. gluteus quartus or scansorius.

Short pubo-ischiofemoral group

M. OBTURATOR INTERNUS (figs. 47, 71). Origin is from the inner surface of the pelvis, overlying the obturator membrane, dorsally as far as the region of the iliopubic junction, and ventrally to the symphysis and downward along its border to the ischial tuberosity. In lateral aspect the muscle appears to be formed of two parts. The major portion converges within the pelvis to a strong tendon that passes dorsally over the superior ramus of the ischium (through the rudimentary lesser sciatic notch) and then ventrolaterally to insertion into the obturator fossa at the medial base of the great trochanter of the femur. Between this tendon and the caudal portion of the gemellus sheet is the lesser portion of the obturator internus. This arises from the medial and mediodorsal borders of the ischial tuberosity and its fibers insert upon the caudal border of the obturator tendon.

MM. GEMELLI (m. gemellus superior and m. gemellus inferior). These form a continuous muscle sheet, not differentiated into the separate superior and inferior elements of human anatomy. The origin extends from a point about one centimeter above the rudimentary ischial spine downward, deep to the m. obturator internus tendon, along the dorsal border of the superior ischial ramus to the tuberosity, and laterally along the upper border of the latter. Insertion is upon both borders and the deep aspect of the tendon of the m. obturator internus.

M. QUADRATUS FEMORIS. This is a thick, quadrilateral muscle that lies caudoventral to the gemellus sheet. It arises from the extreme lateral part of the ischial tuberosity and inserts upon the lesser trochanter or the intertrochanteric crest of the femur. The most dorsal fibers may be segregated to form a separate slip of considerable size that inserts upon the intertrochanteric crest just above the rest of the muscle.

Nerve-supply: The mm. obturator internus, gemelli, and quadratus femoris are all innervated by a nerve component (n.pubo-ischiofemoralis) derived from the ventral rami of nn. lumbales (IV) V-VII. The nerve fibers to this muscular complex may accompany n. flexores femoris for a variable distance.

Action. In man, with upright posture, all of the muscles of this group serve as adductors and lateral rotators of the thigh; but in the usual macaque posture, which is quadrupedal, the group action is probably chiefly that of abduction, with some lateral rotation and weak retraction.

Comparative anatomy. In mammals there is a tendency for this group of muscles to become differentiated from the flexor mass as a separate complex. The m. quadratus femoris is generally present and well developed, but one or more of the remaining divisions may be absent in monotremes, marsupials, and even some placentals. Among primates, including man, one or both of the mm. gemelli may be lacking, or these may exist as a continuous sheet, as in the macaque. The m. obturator internus is regularly present in this order.

MUSCLES OF THE THIGH

Because of the ontogenetic rotation of the lower extremity the primary relationship of the flexors and extensors to the axis of the trunk have become altered. In the anatomical position (B.N.A.) the homologous muscle groups of the two extremities are rotated through 90° in different directions from the embryonic posture and hence have come to lie 180° apart.

Flexor (posterior) group

M. BICEPS FEMORIS (fig. 47). This muscle is actually not bicipital, the short head which arises from the femur in man and some other animals being absent. Origin is rather narrow, from the lateral projection of the ischial tuberosity between the mm. quadratus ~~femoris and~~ semitendinosus. It rapidly increases in both breadth and thickness, and within a short distance additional fibers take origin caudalward by deeper fasciculi. The two portions are partially separable. The broad muscle sheet continues to the lateral side of the thigh, where the anterior muscle fibers are attached extensively to the fascia lata, while the remainder disappear in an aponeurosis that is attached over the anterior border of the leg. The exceedingly broad crural insertion extends for about half the distance to the ankle.

M. SEMITENDINOSUS (fig. 47, 50). From the lateral aspect this muscle borders the posterior region of the thigh. Located posterior to the m. semimembranosus, its origin is more intimately associated with that of the m. biceps femoris. Its fibers arise from the deep fasciculi of the biceps and from the central part of the laterocaudal border of the ischial tuberosity. Passing to the medial border of the calf just deep to the m. gracilis it inserts by a long and rather broad tendon upon a rugosity situated on the anterior surface of the tibia some two to three centimeters below the tuberosity.

M. SEMIMEMBRANOSUS (figs. 47, 48, 50). This is a double muscle composed of two distinct parts, the semimembranosus proprius (also termed m. postsemimembranosus), and the semimembranosus accessorius (sometimes called m. presemimembranosus, or ischiocondyloideus, or portio n. ischiadici m. adductor magnus). The former arises from a point near the laterocaudal border of the ischial tuberosity, between the origins of the mm. semitendinosus and semimembranosus accessorius. It passes down the thigh in close association with, but lateral to, the latter muscle. Its rather narrow and short tendon (which may be seen between the insertions of the mm. semimembranosus accessorius and sartorius) passes under the tibial (medial) collateral ligament to insert upon the medial border of the tuberosity of the tibia and the capsule of the knee-joint. The semimembranosus accessorius arises from the extreme caudoventral termination of the ischial tuberosity ventral to the origin of the semimembranosus proprius. It extends mostly medial to the latter and its fleshy fibers insert broadly upon the femoral shaft medial to the linea aspera, for a distance of several centimeters down to the medial condyle.

Nerve-supply: Mm. biceps, semitendinosus, and both parts of the semimembranosus are supplied by branches of n. flexores femoris.

Action. The muscles of this group are primarily flexors of the leg. When the knee-joint is fixed they retract the thigh. The biceps is also a lateral rotator and perhaps abductor of the thigh, while the semimembranosus and semitendinosus may act as medial rotators.

Comparative anatomy. The m. biceps femoris in mammals is usually represented by only the so-called long head. This is supposed to be derived phylogenetically from two muscles, arising from the vertebral column (caput dorsale m. flexor cruris) and from the ischium (caput ventrale m. flexor cruris), respectively. In some mammals the muscle exhibits the two primitive elements, arising from both vertebral column and ischial tuberosity; in such cases there may rarely be complete separation of the two parts. In numerous forms, however, the long biceps exhibits only the attachment to the ischial tuberosity, the caput dorsale having disappeared; this is the arrangement in primates, but vestiges of the vertebral portion are occasionally encountered. In addition to its normal crural insertion, the long biceps may be inserted partly upon the femoral shaft, as is usual in the orang-utan, or upon the fascia lata, as in the macaque. The so-called short head of the biceps, arising from the femoral shaft and inserting in common with the long head, is found only in some edentates and a few primates (the New World monkeys *Alouatta*, *Lagothrix* and *Ateles*, the anthropoid apes and man). It is apparently a distal part of the gluteal muscle group that has secondarily become associated with the original or long biceps head. Some investigators have attempted to homologize the short biceps head with the m. tenuissimus, a muscle found in numerous mammals.

In many mammals the m. semitendinosus arises by two heads, one from the vertebral column and the other from the ischium, and these two divisions may continue entirely separate. All primates (excepting the lemur *Daubentonia*) possess only the ischial head. In *Tarsius* the muscle is joined in the thigh by the m. gracilis, the two having a common tendon of insertion.

Many mammals have the m. semimembranosus consisting of two parts,—proprius and accessorius. In man the latter has united with the m. adductor magnus, resulting in a compound muscle.

Frequently in mammals, including most primates, the insertions of this flexor, or so-called hamstring, group are more extensive than in man.

Adductor (medial) group

This division (excepting possibly the m. pectineus) is derived from the same portion of the thigh musculature that also gives rise to the flexor group.

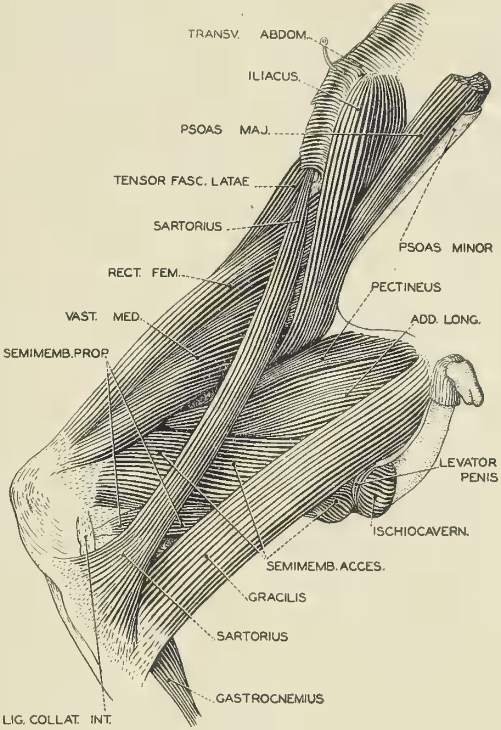

Fig. 48. Muscles of the right thigh, medial view.

M. GRACILIS (fig. 48). This arises from the lateral margin of the symphysis for its cranial half or more. It extends as a ribbon-shaped muscle superficially over the medial aspect of the thigh. Insertion is fibrous upon the anteromedial border to the tibia below the tibial collateral ligament. The posterior part of the insertion covers the m. semitendinosus, while the anterior part is covered by the m. sartorius. *Nerve-supply:* N. obturatorius.

M. ADDUCTOR LONGUS (fig. 48). This muscle arises from the cranial border of the pubis just lateral to the symphysis, between the origins of the mm. gracilis and pectineus. Between the mm. vastus medialis and adductor magnus the muscle fibers disappear, and insertion is entirely aponeurotic upon the linea aspera of the femur for a considerable distance. *Nerve-supply:* N. obturatorius.

M. PECTINEUS (fig. 48). This short, triangular muscle occupies the posterior border of the femoral triangle. It arises from most of the cranial border of the pubis immediately above the obturator foramen. The fibers converge to a tendinous insertion upon the linea aspera for about one-third the length of the femoral shaft. *Nerve-supply:* N. femoralis.

M. ADDUCTOR BREVIS. This lies deep to the m. pectineus and a portion of the m. adductor longus. It arises from the pubis deep to the latter muscle and directly ventral of the obturator foramen. Insertion is between the mm. pectineus and adductor minimus (portion of the m. adductor magnus) upon the upper quarter of the linea aspera. *Nerve-supply:* N. obturatorius.

M. ADDUCTOR MAGNUS (fig. 49). This muscle mass is divisible into two main portions. The perfectly separable medial or anterior division arises deep to the m. gracilis and borders the major extent of the symphysis. It passes between the posterior division and the m. adductor longus to insert upon the linea aspera, for a distance practically coincident with the attachment of the adductor longus, but slightly more distally. The lateral or posterior division is again more or less divisible into several parts. The longest of these originates from the caudal border of the ischial tuberosity immediately cranial to the m. semimembranosus, and inserts upon the posterior aspect of the distal femoral shaft. The intermediate part arises fleshily from the ischium, cranially continuous with the preceding. It inserts upon the middle third or more of the linea aspera. There can also be distinguished a separate upper portion (frequently termed m. adductor minimus), arising from the part of the ischium caudoventral to the obturator foramen. Its relatively short fibers insert upon the lateral part of the linea aspera over approximately the first quarter of the femoral shaft. *Nerve-supply:* The entire muscle receives branches of n. obturatorius.

M. OBTURATOR EXTERNUS. It arises from the lateral border of the obturator foramen and its membrane, backward along the superior ramus of the ischium and the cranial margin of the ischial tuberosity, and forward along the pubis almost as far ventrally as the symphysis. Insertion is by a tendon into the intertrochanteric fossa of the femur. *Nerve-supply:* N. obturatorius.

Action. In considering the actions of the adductor muscles the usual quadrupedal posture of the macaque must constantly be kept in mind. The prime function of this group is adduction of the thigh. All of the muscles, excepting the gracilis, may accomplish lateral rotation; the gracilis is a flexor of the kneejoint and a medial rotator of the thigh when the knee is fixed in flexion. The muscles with more posterior origin can strongly retract the thigh.

Comparative anatomy. The adductor musculature of mammals is subject to a large degree of variation in the extent to which it may be resolved into separate units. In some of the lower mammals an accessory m. gracilis occurs. The m. pectineus is always innervated by the n. femoralis, but in some mammals (as in man) it receives an additional nerve-supply from the n. obturatorius, and the portions supplied by the two nerves may be separate (as in the orang-utan). This muscle component hence presumably may be derived from the extensor musculature alone or from this group and the adductor musculature in addition. The compound condition of the m. adductor magnus in man, with its dual innervation, is attributable to the fusion of the m. semimembranosus accessorius with the primitive adductor magnus element. The m. obturator externus may be double to various degrees in some of the lower mammals.

Extensor (anterior) group

M. SARTORIUS (figs. 47, 48). This is slender and ribbon-like, and is the most superficial muscle upon the medial aspect of the thigh. It arises fleshily from the acetabular border of the ilium a few centimeters caudal to the crest. Insertion is fibrous, for a distance of some three centimeters, chiefly distal to the tibial collateral ligament, over the medial aspect of the tibia.

M. RECTUS FEMORIS (figs. 48–50). This muscle and the three mm. vasti form the so-called m. quadriceps femoris. It arises from the small rectus femoris (ante-acetabular) process which is situated a short distance cranial to the acetabulum along the acetabular border of the ilium. Its fusiform belly passes downward over the m. vastus intermedius to insert upon a common patellar tendon together with the vasti.

M. VASTUS LATERALIS (figs. 49). This is a robust and heavy muscle about three times the mass of the m. rectus femoris. It arises from the entire lateral aspect of the great trochanter of the femur and inserts upon the lateral side of the common patellar tendon and the patella.

M. VASTUS MEDIALIS (fig. 48, 50). Origin is from the medial aspect of the lesser trochanter and from the medial border of the linea aspera for one-third to one-half the length of the femoral shaft. It passes between the mm. adductores and rectus femoris to insert upon the medial part of the common patellar tendon.

M. VASTUS INTERMEDIUS (fig. 49). This is situated between the lateral and medial vastus divisions and deep to the m. rectus femoris. Its fibers arise from the entire anterior aspect of the distal three-quarters of the shaft of the femur. Insertion is upon the deep surface of the common patellar tendon and upon the anterior aspect of the capsule of the knee-joint. There is no separate m. articularis genu. This is represented, however, by the deeper fibers of the vastus intermedius that are attached to the joint capsule.

Nerve-supply: The m. sartorius and the quadriceps femoris group are all innervated by n. femoralis.

Action. All of these muscles extend the leg upon the thigh. The quadriceps complex elevates the patella. The rectus femoris and sartorius are likewise protractors of the thigh. The latter also seems to be capable of some lateral rotation of the knee in the macaque.

Comparative anatomy. The precise point of origin of the m. sartorius is variable. In some mammals it is absent, and it may be replaced by a pseudosartorius developed from the gluteal musculature. At times, as in some primates, including man, the m. rectus femoris has a second head of origin from the margin of the acetabulum, in addition to the usual origin from the ante-acetabular process. The m. articularis genu, as a division of the m. vastus intermedius, is sometimes present in mammals.

MUSCLES OF THE LEG

The leg musculature is divisible into two main groups, one composed of flexors, innervated by ventral elements of the lumbosacral plexus; and the other of extensors, supplied by branches from the dorsal elements of the plexus.

Flexor (posterior) group

M. GASTROCNEMIUS (figs. 47–50). This is composed of two distinct heads, a medial and a lateral. The gastrocnemius medialis arises from the posterior aspect of the femur just above the medial condyle, the gastrocnemius lateralis from a similar area on the lateral side of the bone just above the lateral condyle and in common with the m. plantaris. Each head contains a sesamoid bone just distal to origin. The two heads join somewhat below the middle of the tibia and insert by a common flat tendon upon the posterior aspect of the tuber calcanei.

M. SOLEUS (figs. 49, 50). Origin is by a tendon from the posterior aspect of the head of the fibula and the neighboring surface of the capsule of the knee-joint. At a point about one centimeter above the heel it joins the flat tendon of the m. gastrocnemius on its deep aspect (to form the so-called m. triceps surae), the two muscles inserting upon the tuber calcanei by a common tendon (tendo Achillis).

M. PLANTARIS (fig. 50). This muscle arises in common with, but deep to, the gastrocnemius lateralis, from just above the lateral condyle of the femur. The rather strong and fleshy muscle belly (much weaker, however, than that of the m. gastrocnemius) extends to the lowest quarter of the leg before giving way to a tendon. In its course down the leg it passes beneath the gastrocnemius, and eventually becomes superficial on the medial side of the latter, the tendon passing through a groove in the tendo Achillis over the tuber calcanei to continue in the sole of the foot as the plantar aponeurosis.

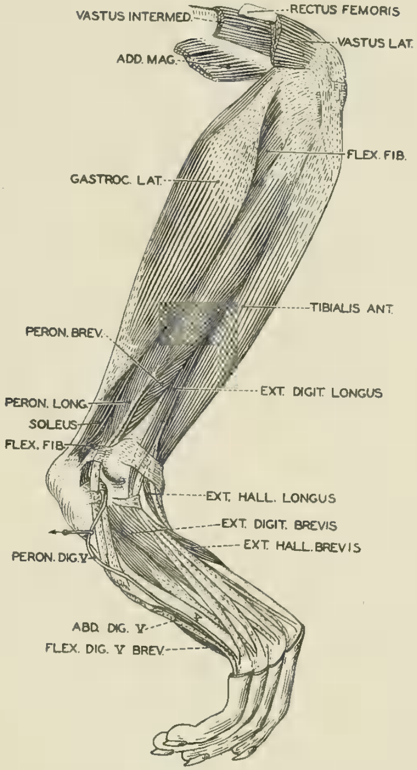

FIG. 49. Muscles of the right leg and dorsum of the foot, lateral view.

M. POPLITEUS (fig. 50). This muscle arises by a narrow but stout tendon from the posterior aspect of the lateral epicondyle of the femur just above the articular surface. The fibers pass medially and downward to a fleshy insertion upon the head of the tibia and distally upon the posteromedial aspect of the shaft for some two-fifths of its extent.

M. PERONEOTIBIALIS. This lies deep to the m. popliteus, and arises from the inner and anterior aspects of the head of the fibula. The fibers spread out to an insertion upon the posterior aspect of the tibia, attachment beginning just below the articular surface and extending downward for nearly two centimeters.

M. FLEXOR DIGITORUM FIBULARIS (figs. 49, 51). This robust muscle, usually termed the m. flexor hallucis longus, arises from the posterior surface of the head and almost the entire shaft of the fibula, from the intermuscular septum between it and the peroneal muscles, from the interosseous membrane between tibia and fibula, and in the lower half of the leg from the adjacent (lateral) border of the tibia. Its tendon passes through the sulcus m. flexoris digitorum fibularis on the posterior aspect of the talus, across the plantar surface of the sustentaculum tali, and in the sole of the foot lies deep (dorsal) to the much smaller tendon of the m. flexor digitorum tibialis. It supplies the major portions of the long flexor tendons to the hallux and the third and fourth toes. These to toes III and IV perforate the corresponding tendons of the m. flexor digitorum brevis and insert upon the plantar surfaces of the terminal phalanges; the tendon to the great toe inserts upon the terminal phalanx.

M. FLEXOR DIGITORUM TIBIALIS (fig. 50). This muscle, also termed the m. flexor digitorum longus, arises from the middle portion of the posterior surface of the tibia. The tendon passes behind the medial malleolus between the tendons of the mm. tibialis posterior and flexor digitorium fibularis and enters the sole of the foot under cover of the laciniate ligament, crossing plantarward of the tendon of the flexor digitorum fibularis. It supplies the long flexor tendons to the second and fifth toes, and sends lesser tendon-slips to join the tendons of the m. flexor digitorum fibularis to the hallux and the third and fourth toes. Its tendons, like those of the long fibular flexor, perforate the corresponding tendons of the m. flexor digitorum brevis and insert upon the plantar surfaces of the terminal phalanges. The insertion of the muscle is subject to some variability, e.g. the contribution to the hallucal tendon may equal that of the long fibular flexor in size, or the slip joining the tendon of the tibial flexor to toe III may be exceedingly small or absent.

M. TIBIALIS POSTERIOR (fig. 50). This is a smaller muscle than the

m. flexor digitorum tibialis. It arises from approximately the upper half of the posterior surface of the tibia, from the interosseous membrane, and from the medial surface of the fibula. The muscle fibers, which attach to the central tendon in a bipennated manner, end about two or three centimeters above the medial malleolus. The narrow tendon passes behind the medial malleolus anterior and medial to that of the m. flexor digitorum tibialis and enters the sole of the foot beneath the laciniate ligament. It inserts upon the inner and under surface of the naviculare by a relatively small process which is prolonged forward to cuneiforme I, but by far the major portion of the tendon is continued into the sole, where it is attached to cuneiformia II and III and the cuboid, forms a part of the sheath of the m. peroneus longus tendon, and inserts upon the bases of the second, third and fourth metatarsals.

Nerve-supply: The eight muscles forming the flexor group of the leg all receive branches of n. tibialis.

Action. Flexion (plantar flexion) of the foot is accomplished chiefly by the gastrocnemius and soleus through their common tendo Achillis, but the long digital flexors and the tibialis posterior play no inconsiderable part in this action. The plantaris tenses the plantar aponeurosis and assists in flexion of the foot. The flexores digitorum fibularis et tibialis flex the digits, with action primarily upon the distal phalanges. The popliteus acts as a medial rotator of the tibia and aids in flexion of the knee; it likewise has an important function in helping to maintain the integrity of the knee-joint. Apparently the sole function of the peroneotibialis is to aid in holding the head of the fibula in apposition to the tibia. Adduction of the foot is also accomplished by the muscles of this group.

Comparative anatomy. The primitive plan of the crural flexors was undoubtedly similar to that of the fore arm flexors. This ideal arrangement, comparable to the present condition encountered in urodele amphibians, includes a tibial and a fibular flexor, a common flexor sheet extending to the digits, and a deeper pronator sheet passing from the fibula to the tibia. The original components have become so altered, however, that their extant representatives can no longer always be recognized with certainty, and the numerous investigations in this field have resulted in widely divergent conclusions. With respect to the Mammalia it seems most reasonable to regard the two heads of the m. gastrocnemius as representing the primitive marginal flexors. Of these, the tibial (gastrocnemius medialis) has remained in a conservative and undifferentiated condition, whereas the fibular (gastrocnemius lateralis) has given rise to two additional muscles, the mm. soleus and plantaris. It should be noted, however, that some investigators regard the two latter muscles as primarily unrelated to the gastrocnemius lateralis, and would derive them from the middle or common flexor sheet. The mm. flexor digitorum fibularis, flexor digitorum tibialis, and tibialis posterior are almost certainly derivatives of the common flexor sheet. The m. flexor digitorum brevis (which is confined to the foot in mammals and is therefore discussed with the plantar muscles) should probably be regarded as one of this group, and thus would represent its more superficial fibers. The allocation of the m. popliteus is uncertain. Some authorities regard it as representing a portion of the primitive pronator layer, but like the humeral head of the m. pronator teres in the upper extremity, it is more probably a division of the original common flexor sheet. Coincident with the loss of the primitive power of pronation and supination in the leg, the pronator stratum has undergone considerable reduction in the placental mammals, being represented only by the inconstant m. peroneotibialis. The m. quadratus plantae, now confined to the foot, possibly, although not certainly, represents the distal portion of the pronator layer; it might, on the other hand, belong to the common flexor group.

The m. gastrocnemius is a conservative muscle in mammals. In the lower members of this class the two heads are usually entirely separate. A true lateral gastrocnemius appears to be missing in monotremes, while in marsupials this head arises from the ligaments of the knee-joint and not from the femur as it does in placentals.

A m. soleus is present in all mammals, arising primitively from the fibula and inserting upon the calcaneus more or less in common with the two heads of the m. gastrocnemius. Among the primates, a second or tibial head is found only occasionally in monkeys and anthropoid apes, and normally in man.

The m. plantaris occurs in most mammals and is usually continuous over the heel with the plantar aponeurosis. It is normally present in prosimians, monkeys and man, but is lacking in gibbons and gorillas, nearly all orang-utans, and a considerable percentage of chimpanzees. In man and the anthropoids (when present) it is much reduced and is attached distally to the tuber calcanei.

A m. popliteus is usually present in mammals. Its structure among the placentals is quite constant, and its variations are of minor interest except in so far as they relate to the question of the possible derivation of the muscle from the pronator sheet.

The m. peroneotibialis (also termed m. pronator tibiae or rotator fibulae) occurs in many mammals. It is met with in some prosimians, in monkeys and gibbons, and occasionally in the great apes and man.

The mm. flexores digitorum fibularis et tibialis primitively are fused in the sole, and each component sends tendon slips to all five digits. The various types of insertion of these two muscles in mammals are but modifications of this arrangement and the exact distribution of the tendons is subject to much generic and individual variation. Most prosimians and many monkeys adhere in general to the primitive mammalian scheme, but in the three great apes there is a marked tendency for the tendons of the two flexors to become separated, the fibular supplying the first, third and fourth digits, the tibial the second and fifth. In the orang-utan the hallucal tendon is nearly always lacking. The conditions in gibbon and man are more primitive than those occurring in the three great apes.

The variations of the m. tibialis posterior are of no great interest. In most prosimians the insertion of the muscle is confined to the naviculare, but in the other primates it sends tendinous slips to attach to the sheath of the m. peroneus longus tendon and some of the tarsal and metatarsal bones in addition to its naviculare insertion.

Extensor (anterior) group

The first three of these muscles comprise the anterior extensor division, innervated by the deep peroneal nerve, and the last three the lateral or peroneal group, supplied by the superficial peroneal nerve.

M. TIBIALIS ANTERIOR (figs. 49, 50). It is a large and well developed muscle. Origin is from the lateral condyle of the tibia, from the lateral surface of that bone, and from the interosseous membrane. The muscle belly soon splits into longitudinal halves. The more robust medial half gives rise to a well developed tendon that passes beneath the transverse crural ligament and inserts upon the medial and plantar aspects of cuneiforme I. The lateral half produces a smaller tendon that accompanies the tendon of the medial belly for most of its course, and inserts upon the medial plantar surface of the base of the hallucal metatarsal. The latter portion is sometimes termed a separate muscle, the m. abductor hallucis longus.

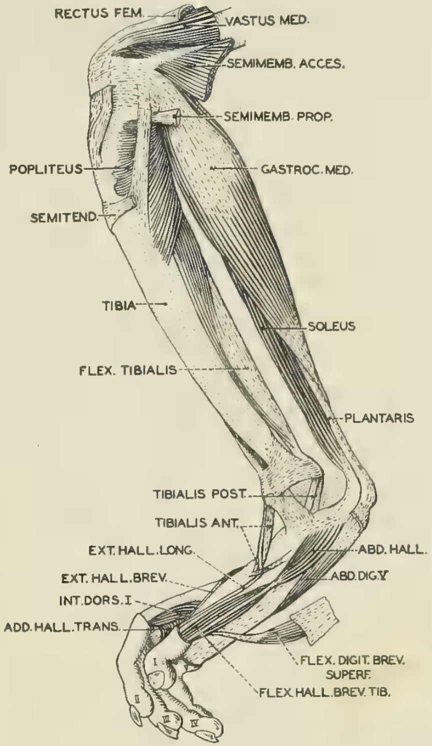

Fig. 50. Muscles of the right leg and foot, medial view.

M. extensor hallucis longus (figs. 49, 50). Origin of this small muscle is from approximately the middle third of the medial surface of the fibula and from the interosseous membrane. The muscle fibers extend quite to the foot. The tendon (of about the same size as the lateral tendon of the m. tibialis anterior) runs under the transverse crural ligament to the medial side of the foot, passes beneath a bridge formed by a portion of the dorsal naviculo-entocuneiform ligament, and curving around the plantar border of the latter attains the dorsum of the hallux to insert by a dorsal expansion upon both phalanges.

M. EXTENSOR DIGITORUM LONGUS (fig. 49). This muscle is smaller than the m. tibialis anterior, but larger than the m. extensor hallucis longus. It arises fleshily from the lateral condyle of the tibia, from the head and proximal three-fourths of the anterior surface of the fibula, from the interosseous membrane, and from the septum separating it from the peroneal muscles. The muscle fibers extend to the foot. Three tendons develop in the leg. These pass beneath the transverse crural ligament to the dorsum of the foot, where they run through a sling-like ligament which arises in the sinus tarsi. The lateral tendon goes to the dorsum of the fifth toe, the intermediate to the dorsum of the fourth toe, and the medial divides beyond the middle of metatarsale III into tendons destined for the dorsal surfaces of the third and second toes respectively. Insertion of each tendon is chiefly upon the middle phalanx, with some fibers passing to the terminal phalanx.

M. peroneus tertius is absent.

Nerve-supply: The three anterior extensor muscles are supplied by n. peroneus profundus.

M. PERONEUS LONGUS (fig. 49). Origin is from the lateral intermuscular septum, lateral aspect of the upper third of the shaft of the fibula, head of the fibula, and lateral aspect of the head of the tibia just forward of the fibular collateral ligament. The tendon passes downward lateral to those of the mm. peroneus brevis and peroneus digiti quinti, and behind the lateral malleolus beneath the peroneal retinacula. It curves around the lateral border of the cuboid, where it contains a large sesamoid bone, and crosses the sole of the foot under cover of a tendinous sheath formed by the plantar ligaments and the tendon of the m. tibialis posterior, to insert upon the lateral plantar aspect of the base of the hallucal metatarsal bone. In addition to the main insertion there may be a secondary attachment by a small tendinous slip to the base of the fifth metatarsal or to both this bone and the cuboid; this accessory tendon, when present, is given off by the main tendon of the peroneus longus as it enters the sole.

M. PERONEUS BREVIS (fig. 49). This arises from the lateral surface of the fibula and the adjacent intermuscular septa. Its tendon passes behind the lateral malleolus and beneath the peroneal retinacula, medial to that of the m. peroneus longus. Insertion is upon the tuberosity of the fifth metatarsal bone.

✓ M. PERONEUS DIGITI QUINTI (fig. 49). Origin of this small muscle is by a slender belly from the upper part of the posterolateral edge of the fibular shaft adjoining the m. peroneus brevis. The slender tendon runs between the mm. peroneus brevis and peroneus longus, behind the lateral malleous through the peroneal retinacula, and, crossing the tendon of the peroneus brevis, lies dorsal to the latter in the foot. It is continued forward over the dorsal aspect of the fifth metatarsal bone to insert upon the lateral side of the fifth toe, reaching the terminal phalanx.

Nerve-supply: All three peroneal muscles are innervated by n. peroneus superficialis.

Action. The tibialis anterior and the long extensors of the toes produce extension (dorsal flexion) of the foot. The former likewise inverts the foot, and through its attachment to the first metatarsal bone it abducts the hallux. The long digital extensors extend the toes; the peroneus digiti quinti acts similarly upon the fifth toe, and abducts it somewhat as well. Eversion of the foot is accomplished by the peroneus brevis and the peroneus longus. Both of these muscles are so situated as to aid in flexion of the foot. The peroneus longus, in addition, is a strong flexor of the hallux, its action being such as to oppose the great toe to the other digits. The muscles of this group likewise abduct the foot.

Comparative anatomy. The crural extensors seem to have departed less from the primitive plan than have the corresponding flexors. The ideal arrangement includes a tibial and a fibular extensor, a common extensor sheet to the digits, and a deeper supinator layer passing from fibula to tibia. Of these the m. tibialis anterior represents the tibial extensor and the several peroneal muscles the fibular extensor. The former is a rather conservative muscle in mammals, but the original fibular extensor has undergone differentiation into several elements, comprising the m. peroneus longus, m. peroneus brevis, and a variable number of peroneal digital extensors. The middle or common extensor sheet exhibits no splitting into superficial and deep divisions, passing to all five digits as the mm. extensores digitorum et hallucis longi. The supinator stratum has completely disappeared in mammals.

The m. tibialis anterior is generally undivided in mammals, and usually inserts upon the medial side of the tarsus or upon metatarsale I. In prosimians the insertion is either simply upon cuneiforme I or else the muscle is divided, the two parts attaching to the first cuneiform and to the hallucal metatarsal respectively. The latter condition occurs in practically all monkeys and anthropoid apes, but there is considerable variability in the extent to which the muscle is divided. This division may involve only the terminal tendon, or it may be so extreme as to separate the entire muscle into longitudinal halves. Accessory insertions sometimes occur. In man the muscle usually has a single tendon of insertion upon cuneiform and metatarsal, but splitting of the tendon, or even of the muscle belly, may be encountered.

The primitive insertion of the m. peroneus longus was undoubtedly upon the lateral border of the foot, and its usual mammalian attachment to the first metatarsal bone is the result of a migration across the sole of the foot. Secondary insertions upon the fifth metatarsal, or even upon other bones, are not rare. In primates insertion usually is limited to the hallucal metatarsal, but there is frequently an atavistic accessory slip to the fifth metatarsal or cuboid, or even, as is normal in man, a progressive attachment to the first cuneiform.

The m. peroneus brevis is a conservative muscle. In most mammals it inserts upon metatarsale V. Its variations are of no particular interest, except as they pertain to the association of the muscle or its tendon with the m. peroneus digiti quinti.

The peroneal digital extensors are usually two in number, one for the fifth toe (m. peroneus digiti quinti) and one for the fourth (m. peroneus digiti quarti). The former regularly occurs in lower primates, and the latter is also often present. The latter has disappeared in the anthropoid apes and man, but a vestige of the quinti, in the form of a slender tendon prolonged distally from that of the peroneus brevis, is not infrequently encountered. The more or less complete muscle may occasionally occur in these forms.

The variations of the mm. extensores digitorum et hallucis longi relate chiefly to the absence of one or more of the terminal tendons, to their connections with one another, and to accessory slips. The m. extensor hallucis longus in man not infrequently furnishes an accessory tendon to the basal phalanx of the hallux (termed m. extensor primi internodii hallucis). In man, not uncommonly in gorillas and rarely in chimpanzees, there is developed from the lateral portion of the m. extensor digitorum longus a m. peroneus tertius, which inserts upon the lateral border of the metatarsus.

MUSCLES OF THE FOOT

As in the remainder of the limb, the intrinsic foot musculature is divisible into a plantar flexor group and a dorsal extensor one, innervated respectively by ventral and dorsal elements of the lumbosacral plexus.

Flexor (*plantar*) *group*

The *aponeurosis plantaris* (fig. 50) is the plantar continuation of the tendon of the m. plantaris. It spreads out to cover the plantar muscles, extending toward the distal end of the metatarsus. Along the margins of the foot it becomes weaker and tends to disappear. It gives off slips to some of the deeper structures of the sole.

M. FLEXOR DIGITORUM BREVIS (figs. 50, 51). This muscle is composed of two distinct heads. The superficial head arises fleshily from the deep surface of the plantar aponeurosis (and in some specimens also from the medial portion of the tuber calcanei adjoining the abductors of the first and fifth digits) and inserts upon the plantar surface of the middle phalanx of the second toe. The deep head arises as a muscle belly attached to the undivided tendon of the m. flexor digitorum tibialis, extending from about the lower level of the medial malleolus into the sole, where it gives rise to three tendons, inserting respectively upon the plantar surfaces of the middle phalanges of the third, fourth and fifth toes. The tendons of both heads are perforated by the corresponding tendons of the long digital flexors. The muscle is subject to some variability in respect to the toes supplied by the two heads.

For example, the superficial head may occasionally produce an extra tendon which joins that proceeding from the deep head to the third toe. *Nerve-supply:* Both heads are innervated by n. plantaris medialis.

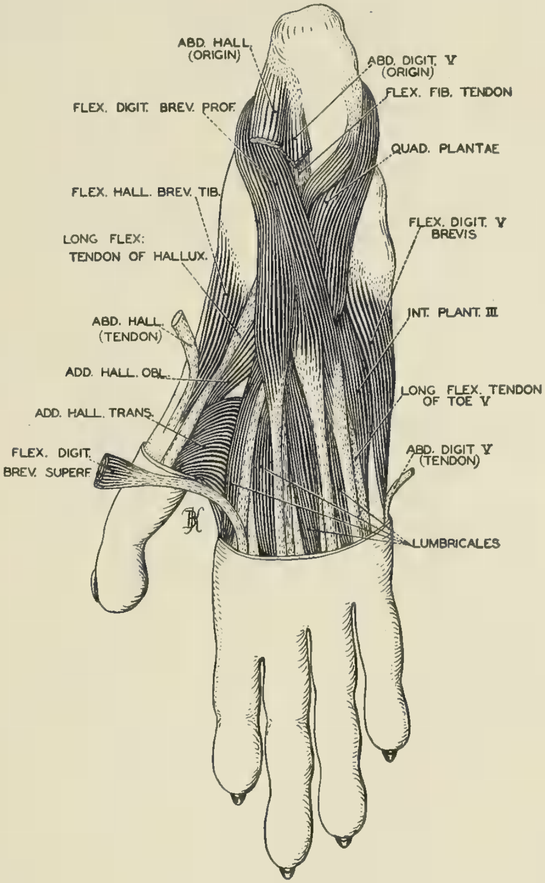

Fig. 51. The more superficial plantar muscles of the right foot. The plantar aponeurosis has been removed.

M. abductor hallucis (figs. 50, 51). This arises from the more medial portion of the tuber calcanei and the deep surface of the plantar aponeurosis. Insertion is together with the medial head of the m. flexor hallucis brevis upon the tibial side of the basal phalanx of the great toe. *Nerve-supply:* N. plantaris medialis.

M. flexor hallucis brevis (figs. 50–52). This muscle is composed of two heads. The medial head arises from the naviculare and cuneiforme I (with occasional fibers from the first metatarsal also) and inserts together with the m. abductor hallucis upon the medial side of the basal phalanx and metatarsophalangeal joint capsule of the hallux. The much smaller lateral head is pressed into the sole, and is covered superficially by the long flexor tendon of the hallux, which passes just lateral to the medial head. It arises from cuneiforme I (and sometimes also from the proximal part of the hallucal metatarsal bone) and inserts together with the oblique head of the m. adductor hallucis upon the lateral side of the basal phalanx and metatarsophalangeal joint capsule of the hallux. *Nerve-supply:* N. plantaris medialis.

M. ADDUCTOR HALLUCIS (figs. 50–52). This muscle consists of two heads. The transverse head arises from the heads and joint capsules of metatarsalia II and (less strongly) III, from along the medial border of m. contrahens digiti IV, and from the fascia over m. contrahens digiti II. There is some variability in the origin of the transverse head, which may extend to metatarsale IV, or be limited to metatarsale II. Insertion is fleshily upon the lateral side of the basal phalanx of the hallux as far as the last joint; the muscular fibers may extend upon the last phalanx itself. The oblique head, usually separated by a small interval from the preceding, arises from the common aponeurosis of the contrahentes muscles and from the bases of metatarsalia II and III. Insertion is together with the lateral head of the m. flexor hallucis brevis upon the lateral side of the metatarsophalangeal joint capsule and basal phalanx of the hallux, and continued forward to join those of the transverse head, while deeper fibers insert upon the lateral aspect of the head of the hallucal metatarsal bone. *Nerve-supply:* Ramus profundus n. plantaris lateralis

M. ABDUCTOR DIGITI QUINTI PEDIS (figs. 49–51). Origin is from the tuber calcanei lateral to that of the m. abductor hallucis, and from the deep surface of the plantar aponeurosis. Insertion is upon the lateral side of the basal phalanx of the fifth toe. In some specimens the more lateral fibers separate to insert upon the tuberosity of the fifth metatarsal bone, forming a m. abductor ossis metatarsi quinti. *Nerve-supply:* N. plantaris lateralis.

M. ABDUCTOR OSSIS METATARSI QUINTI. This muscle, when present, merely represents the lateral fibers of the m. abductor digiti quinti inserting upon the tuberosity of metatarsale V. *Nerve-supply:* N. plantaris lateralis.

M. FLEXOR DIGITI QUINTI BREVIS PEDIS (figs. 49, 51, 52). Origin is from the sheath of the m. peroneus longus tendon and the base of the fifth metatarsal bone. Insertion is upon the lateral side of the basal phalanx of the fifth toe. *Nerve-supply:* N. plantaris lateralis (either ramus superficialis or ramus profundus).

M. opponens digiti quinti pedis is normally absent.

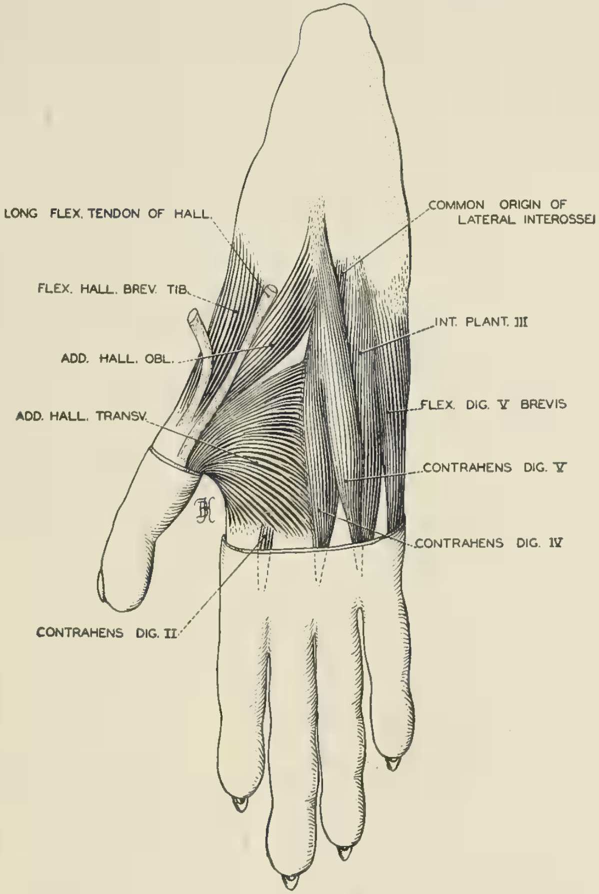

Fig. 52. The deeper plantar muscles of the right foot.

M. QUADRATUS PLANTAE (fig. 51). This muscle arises by a single head, from the lateral side of the calcaneus just behind the tendon of the m. peroneus longus and adjacent to the inferior peroneal retinaculum. It inserts by a small fleshy slip upon the lateral side of the long flexor tendon of the fifth toe, and by tendinous slips contributing to the formation of a variable number of long flexor tendons. These tendinous slips usually go to all five long flexor tendons, but those destined for toes III and IV may be missing. The fleshy insertion may likewise be lacking, insertion in such instances being entirely tendinous. *Nerve-supply:* N. plantaris lateralis.

Mm. lumbricales pedis (fig. 51). These are four in number. They arise in the sole by two heads from the adjacent surfaces of the long flexor tendons, the most medial lumbrical excepted; the latter takes origin from only the medial side of the long flexor tendon of the second toe. The four muscles insert upon the medial sides of the basal phalanges of the second to fifth toes, each tendon being prolonged to the dorsum of its toe, where it reaches the medial side of the terminal phalanx. *Nerve-supply:* Innervation is variable, but always from the nn. plantares; the mm. lumbricales of toes II and III are usually supplied by the n. plantaris medialis, those of toes IV and V usually by the n. plantaris lateralis.

Mm. contrahentes digitorum pedis (fig. 52). These muscles are three in number. They arise from a common aponeurotic tendon attached to the sheath of the m. peroneus longus tendon. This aponeurosis gives rise to three muscle bellies that insert upon the basal phalanges respectively of toes V (medial side), IV (medial side), and II (lateral side). The contrahens of the second toe is usually almost entirely covered by the fibers of the transverse adductor of the hallux. The contrahentes belong to the same muscle sheet as the m. adductor hallucis, the latter muscle being really the contrahens of the great toe. *Nerve-supply:* Ramus profundus n. plantaris lateralis, which passes between the contrahentes and the interosseous muscles.

Mm. interossei pedis (figs. 50–52). These are seven in number, four dorsal and three plantar. The muscles arise in two usually distinct groups, a medial and a lateral. The medial group is composed of three muscles (first dorsal, first plantar, and second dorsal interossei) having a common origin from the plantar aspect of the base of the second metatarsal bone and the adjacent portion of the sheath of the m. peroneus longus tendon. The lateral group is composed of four muscles (third dorsal, second plantar, fourth dorsal, and third plantar interossei) which arise together (and with the m. flexor digiti quinti brevis) from the plantar surface of the bases of the fourth and fifth metatarsals and the adjacent part of the sheath of the m. peroneus longus tendon. The plantar surface of the third metatarsal bone thus typically gives rise to no interosseous fibers. In some instances, however, the two groups are of different composition or are not so well separated, and a part of one or both of the interossei of the third digit may take origin from metatarsale III. Origin of the interossei from the shafts of the metatarsals is slight, being usually weakly fibrous. The dorsals (excepting the first) may have additional heads of origin from the adjacent surfaces of the shafts of the metatarsals bounding their respective interosseous spaces, but these attachments are likewise usually weakly fibrous in nature. All seven interossei insert upon the sides of the basal phalanges of the four lateral toes, with extensions to the corresponding tendons of the m. extensor digitorum longus. The first plantar goes to toe II (lateral), the second plantar to toe IV (medial), and the third plantar to toe V (medial). The first dorsal goes to toe II (medial), the second dorsal to toe III (medial), the third dorsal to toe III (lateral), and the fourth dorsal to toe IV (lateral). The only real distinction between the dorsals and the plantars lies in their relative positions, for only the former (although they are not entirely dorsal) can be seen from the dorsum of the foot. The second dorsal interosseous is usually the most plantar in position. There is some slight tendency for the plantar portions of the four dorsal muscles to be split off to form additional plantar interossei, but this process is by no means as marked as in the hand. The orientation of the dorsal interossei is, as in the hand, with reference to an axis through the third digit. This differs from their arrangement in the foot of man, in which the axis is through the second digit. *Nerve-supply:* All of the interosseous muscles are regularly innervated by ramus profundus n. plantaris lateralis. In some specimens, however, the muscles of the outermost interosseous space (fourth dorsal and third plantar) receive their innervation from ramus superficialis n. plantaris lateralis.

Action. The flexor digitorum brevis flexes primarily the second phalanges of the four lateral toes, the action of the deep head being strengthened by the movable base (tendon of flexor digitorum tibialis) to which it is attached. The dorsal interossei abduct the second, third and fourth toes from an axis through the middle digit, while the plantar interossei and the contrahentes digitorum adduct the second, fourth and fifth toes to this axis. All of the interossei and contrahentes, together with the lumbricales and the flexor digiti quinti brevis, flex the first phalanges of the four lateral toes. The lumbricales, and probably the interossei also, aid in the extension of the more distal segments of the digits. The abductors of the hallux and fifth toe abduct their respective digits from the midline of the foot. Flexion of the first hallucal phalanx is produced by the flexor hallucis brevis, aided by the abductor hallucis. The adductor hallucis, as a member of the contrahentes group, adducts the great toe toward the midline of the foot, while together with the flexor hallucis brevis it assists the peroneus longus in production of the complex action of hallucal opposition. The quadratus plantae, by its lateral pull, counteracts the medial pull of the long flexor muscles, the resultant action being more nearly in line with the long axis of the foot; through its tendinous attachments to the separate digital tendons of the long flexors it aids in flexion of the toes.

Comparative anatomy. The m. flexor digitorum brevis is a highly variable muscle. In mammals it commonly is composed of two heads,—namely, a superficial head arising from the plantar aponeurosis (and at times from the calcaneus as well) and a deep head taking origin from the tendon of the m. flexor digitorum tibialis. The number of tendons supplied by each head, and their exact digital distribution, are features which are subject to considerable ordinal and even generic and individual variability. In the primitive primate arrangement the superficial head furnishes a tendon to the second toe alone, while the deep head supplies the third, fourth and fifth digits. Within this order there is a rather progressive disappearance of the deep head through transference of its tendons to a superficial origin. The culmination of this process occurs in man, in whom all four tendons normally are products of the superficial head. The most common arrangement among prosimians, monkeys and gibbons is the primitive one in which the superficial head supplies only the second toe. The great apes, on the average, are intermediate between the lower primates and man, the closest approach to the human condition being made by the orang-utan. Occasionally in man a deep head may be present; in such instances it is represented by the lateral tendons, particularly that of the fifth toe, which arise from a muscle belly attached to the m. flexor tibialis tendon. There is a progressive tendency for the tendon of the fifth toe to disappear. This tendon is only occasionally absent in Old World monkeys, but it is quite frequently lacking in gibbons and man, is even more commonly absent in orang-utans and gorillas, and is missing in a majority of chimpanzees.

The short muscles of the hallux and fifth toe may exhibit a number of variations, chiefly of minor interest. The m. adductor hallucis frequently has a partial metatarsal insertion in primates, and may be fused with the lateral head of the m. flexor hallucis brevis. A m. opponens hallucis may occasionally be derived from the medial head of the m. flexor hallucis brevis (or even from the m. abductor hallucis). Among primates this muscle normally occurs only in the orang-utan. The m. abductor digiti quinti frequently gives rise to a m. abductor ossis metatarsi quinti. A m. opponens digiti quinti, derived from the m. flexor digiti quinti brevis, likewise is not uncommon.

The m. quadratus plantae is most probably an extrinsic muscle of the foot which has settled down secondarily to a pedal origin. It is normally lacking in some of the lower mammals (some insectivores, most bats, ungulates, some edentates, carnivores and rodents, and most marsupials). When present it commonly arises by a single head from the lateral border of the foot. The second head of man has apparently been caused by a medial migration of some of its fibers. The muscle is consistently absent in prosimians (but has been found in *Tarsius*), occurs regularly in monkeys, is lacking always in gibbons, is missing very frequently in chimpanzees, is usually absent in orang-utans and gorillas, and is but rarely absent in man. It furnishes a variable number of slips to the tendons of the long flexor muscles. A primitive crural origin is occasionally encountered in man.

The mm. lumbricales are subject to the same types of variations as are the corresponding muscles of the hand (see page 148).

The original arrangement of the mm. contrahentes digitorum parallels that of their homologues in the hand. Primitively there are four muscles inserting upon the first (m. adductor hallucis), second, fourth and fifth digits, respectively, with adducting action toward an axis through the third toe. This is the arrangement found in monkeys. In prosimians there is a tendency for the contrahens of the fourth toe to be absent. Reduction or disappearance of the three lateral contrahentes occurs in the gibbons and the chimpanzee, is farther advanced in the orang-utan, and is normally complete in the gorilla and man. The most medial member of the contrahentes, the m. adductor hallucis, is normally present and strong in all primates. Its transverse head is the product of a migration of some of its fibers distally to the end of the metatarsus.

The mm. interossei, like those of the hand, are derived from the mm. flexores breves profundi of lower tetrapods. The four dorsal muscles are primitively oriented with reference to an axis through the third toe. This is the condition in all monkeys and in some prosimians, but in others of the latter group the axis has shifted to the fourth digit. The axis passes primitively through the third toe in most gibbons, chimpanzees and orang-utans, but in occasional specimens of all three forms it has shifted medially to the second toe, the latter condition being normal for both man and gorilla.

Extensor (dorsal) group

M. EXTENSOR DIGITORUM ET HALLUCIS BREVIS (figs. 49, 50) is the single muscle making up this group. It arises from the lateral and dorsal sides of the calcaneus. It divides into four bellies which insert respectively upon the lateral sides of the dorsal surfaces of toes IV, III and II, the tendons reaching the terminal phalanges, and upon the lateral side of the dorsum of the basal phalanx of the hallux. The bellies for toes I and II are connected distally by a tendinous arch. *Nerve-supply:* N. peroneus profundus.

Action. The extensor digitorum et hallucis brevis extends the four medial toes and abducts them lateralward.

Comparative anatomy. The m. extensor digitorum et hallucis brevis is probably the intrinsic extensor of the foot, although some investigators have considered it as derived from the peroneal musculature and have regarded its pedal origin as secondary. The short extensor of the foot is subject to a relatively great degree of variability in mammals. Some of the bellies or tendons may be lacking, or the slips to one or more toes may be doubled. Practically all such types of variations are to be encountered among prosimians, but in monkeys, apes and man the usual condition is one in which a separate tendon passes to each of the four medial digits. A tendon to the fifth toe is only very occasionally present, but an extra tendon to the second toe seems to occur regularly in at least some New World monkeys.

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Chapter VIII

THE FACIAL MUSCULATURE AND ITS INNERVATION

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The facial musculature of the rhesus macaque, embracing all the muscles innervated by the n. facialis, can be subdivided into:

I. *Superficial facial musculature*, represented by the m. platysma colli et faciei, mimetic muscles of the face, superficial muscles of the cranial vault, and extrinsic and intrinsic outer ear muscles.

II. *Deep facial musculature*, represented by the m. stapedius (see chapter XVIII), posterior belly of the m. digastricus and m. stylohyoideus (see chapter VII).

This section deals with the plan of the *superficial facial musculature* of the rhesus macaque, with consideration of some of the numerous individual variations which may be encountered in this muscle group.

Through broad comparative anatomical investigations the superficial facial muscles have been traced back to a primitive transverse muscle layer located in the neck region. In the phylogeny of the mammals this "primitive sphincter colli" has given rise to the platysma and the sphincter colli profundus. From these two matrix layers the various muscle groups and individual superficial facial muscles have evolved through gradual differentiation. It may be stated briefly that the m. platysma colli et faciei and the entire postauriculo-occipital muscle group, including a series of extrinsic and intrinsic outer ear muscles, were derived from the platysma, while the rest of the superficial facial musculature (i.e. the muscles of the anterior part of the cranial vault, the pre-auricular muscle complex, and the muscles of the face proper) were derived from the sphincter colli profundus. Since the matrix layers were innervated by the n. facialis, all the muscles which have evolved from these, i.e. the entire superficial facial musculature, are now supplied by branches of the n. facialis.

In order to gain a clear understanding of the plan of the superficial musculature in the rhesus macaque and a sound basis for the evaluation of individual variations which may be encountered in this animal, it is necessary to have some appreciation of the evolution of facial musculature in the "ascending scale of the primates." An introduction to this subject is given in the 3rd chapter of the author's book on the "Evolution of Facial Musculature and Facial Expression," 1931, to which the reader is referred.

In the following presentation the superficial facial muscles of the rhesus monkey will be discussed according to their derivation from the two matrix layers, the platysma and the sphincter colli profundus:

A. THE PLATYSMA AND ITS DERIVATIVES

m. platysma colli et faciei
postauriculo-occipital muscle group:
    m. occipitalis
    m. auricularis posterior
    m. auricularis anterior et superior (posterior section)
    mm. auriculares proprii
        mm. obliqui et transversi
        m. antitragicus
        m. helicis (minor)
        m. mandibulo-auricularis (occasional vestiges)

M. platysma colli et faciei arises in a primitive manner from the nuchal region and from over the shoulder (fig. 53, A and B). From there it passes below the ear into the face, extending oralward as far as the lower lip (fig. 53B). While deep platysma bundles attach themselves to the mandible, the lower lip portion is not differentiated as a distinct m. quadratus labii inferioris as in the great anthropoid apes and man.

The platysma colli et faciei shows some noteworthy modifications which are undoubtedly correlated with the possession of a buccal pouch (fig. 54, A and B), which is characteristic not only of the rhesus monkey but of all the representatives of the Cercopithecinae. This buccal pouch is formed by a continuation of the mucous membrane of the cheek-wall covered with a strong muscular coat derived from the m. buccinator. It has herniated through the platysma, splitting this muscle plate into an upper and a lower portion (figs. 53B; 54, A and C) which are distinct for the entire extent of the muscle as far as its origin in the nuchal region (fig. 53, A and B). The buccal pouch rests upon the lower portion of the platysma subjacent to the skin (figs. 53B; 54, A and C). Anterior to the pouch strong bundles of the platysma crossing from the right and left sides interlace (figs. 53A, 54C). This solid interlacing of platysma bundles below the chin is, no doubt, likewise correlated with the formation of the buccal pouch. Of merely accessory nature, on the other hand, is the splitting off from the platysma of a series of insignificant muscle bundles over the upper part of the chest (figs. 53B, 54C).

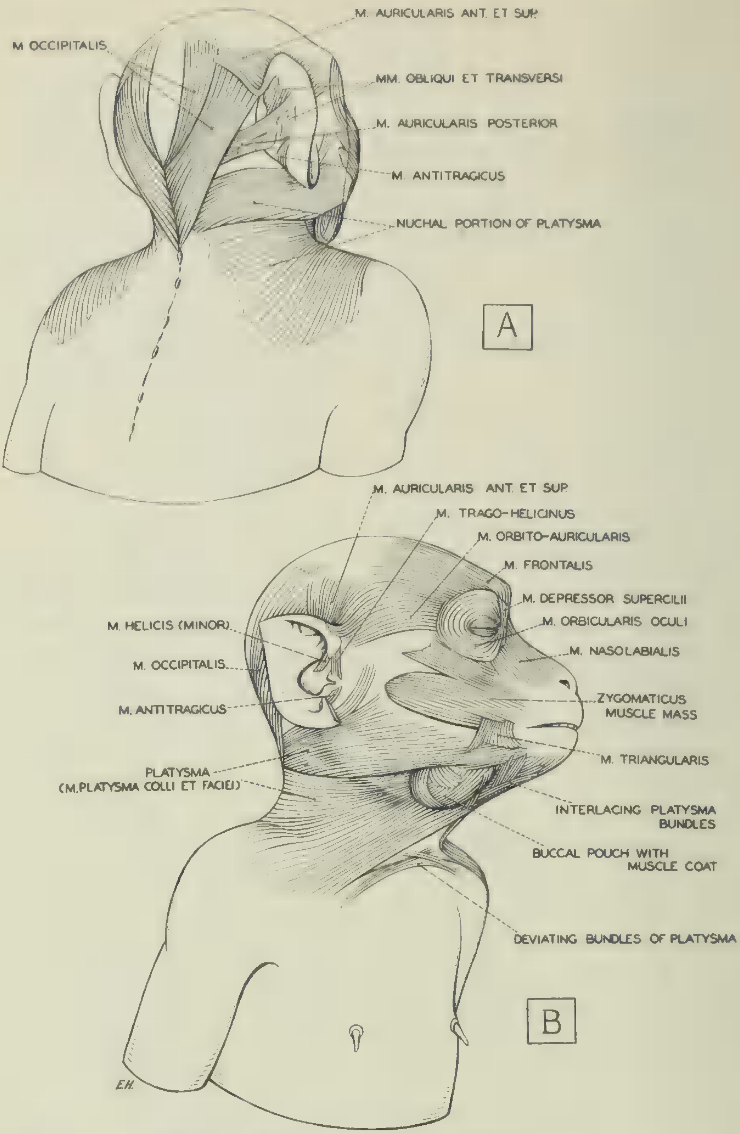

FIG. 53. The superficial facial musculature. (Drawn by E. Huber.)

A, posterior view, to show the postauriculo-occipital muscle group in genetic relation with its matrix, the nuchal portion of the platysma.

B, side view, to show the general arrangement of the superficial facial musculature. (1) M. platysma colli et faciei and postauriculo-occipital musculature, of which are seen the m. occipitalis, the posterior section of the m. auricularis ant. et sup., and two of the intrinsic ear muscles, the m. helicis and the m. antitragicus. (2) The rest of the muscles of the anterior part of the cranial vault and face, and of the buccal pouch, representing derivatives of the sphincter colli profundus (see further fig. 54, A and B).

The postauriculo-occipital muscle group has retained a close connection with the nuchal portion of the platysma (fig. 53A) from which it is derived. These primitive conditions are thus in striking contrast with those found in the great anthropoid apes and man, where the genetic relationship of the postauriculo-occipital musculature to the platysma has become obscured through deterioration of the nuchal platysma, vestiges of which are preserved in the inconstant and very variable m. transversus nuchae. M. occipitalis largely arises from the spinous processes of the lower cervical vertebrae, the ligamentum nuchae and the occiput, and is inserted above into the freely movable galea aponeurotica. In a primitive way the lateral bundles of this muscle plate frequently insert into the outer ear, thus making the muscle a m. occipito-auricularis. From this main layer of the m. occipitalis is differentiated a deeper occipitalis layer which has a separate origin from the external occipital protuberance and a small area of the superior nuchal line in the same plane with the m. auricularis posterior (fig. 55A). It is partly covered by the medial border of the superficial, main layer of the m. occipitalis (figs. 53A, 55A). The interspace between the occipital musculature of the two sides may be much smaller than in the examples shown in these figures. At times the two bilateral muscles almost join in the midline, while in other specimens they join and even overlap at their insertion above.

The m. auricularis posterior arises chiefly tendinously, from the superior nuchal line lateral to the deep layer of the m. occipitalis (fig. 55A). Under cover of the superficial layer of the m. occipitalis it passes toward the ear (fig. 53A), where it inserts with two slips into the eminentia conchae. There, some of its bundles may be continuous with the mm. obliqui et transversi which have settled down on the convex surface of the ear cartilage, thus forming part of the intrinsic outer ear musculature. The posterior section of the m. auricularis anterior et superior (fig. 53A) also is to be included in the postauricular muscle complex, as evidenced by its innervation through a postauricular branch of the n. facialis (fig. 55A). It has become fused with a portion derived from the pre-auricular muscle complex (see innervation, fig. 55B) to produce a uniform muscle.

Among the intrinsic postauricular muscles the mm. obliqui et transversi are of greatest extent. While retaining a primitive connection with their matrix muscle, the m. auricularis posterior, they have expanded over a large area of the convex surface of the ear cartilage, here bridging the fissure which corresponds to the anthelix on the concave surface of the ear (fig. 53A). They are, however, not further subdivided into a m. transversus auriculae and a m. obliquus auriculae as they are in man. Through migration from the convex surface of the ear cartilage (fig. 53A) to the antigragus of the ear a portion of the mm. obliqui et transversi has given rise to the m. antitragicus (fig. 53, A and B). This still retains its primitive connection with its matrix (fig. 53A). The m. helicis (figs. 53B and 55C) likewise has evolved from the mm. obliqui et transversi, being the product of a portion which has migrated from the convex surface of the ear cartilage to the anterior border of the ear. While it has lost connection with its matrix and is now completely isolated on the crus helicis, the characteristic innervation through a post-auricular branch of the n. facialis (fig. 55B) still clearly indicates its source of origin. This muscle is homologous to the m. helicis minor of man, but there is no m. helicis major in the rhesus monkey. As a rare primitive variation there may be found in the macaque vestiges of the m. mandibulo-auricularis (fig. 55C), an ear muscle which is still normally present and functioning in the prosimians and which is characteristic of the ground-plan of the placentals and marsupials. It has evolved from the m. helicis by migration of muscle bundles along the cartilaginous ear tube to the mandible (see Huber 1925, and 1925/26).

B. THE DERIVATIVES OF THE SPHINCTER COLLI PROFUNDUS

1. Derivatives of the pars pre-auricularis
    - pre-auriculo-temporo-frontal muscle complex:
        - m. auricularis anterior et superior (anterior section)
        - orbito-auricular muscle plate
        - m. frontalis
    - m. tragohelicinus
    - zygomatico-orbital muscle mass
    - m. orbicularis oculi
    - m. depressor supercilii
    - m. corrugator supercilii
    - m. nasolabialis
2. Derivatives of the pars oris
    - orbicularis oris-buccinator system:
        - m. orbicularis oris
        - m. caninus
        - m. triangularis
        - m. buccinator
    - m. mentalis
    - m. levator labii superioris proprius

The sphincter colli profundus as a matrix layer has disappeared from the plan of the facial musculature of the rhesus macaque. Vestiges of it occasionally may be encountered as primitive variations. The derivatives of the sphincter colli profundus, however, are well developed though not greatly differentiated.

The m. auricularis anterior et superior, the orbito-auricular muscle plate and the m. frontalis still form a primitive muscle complex which covers the anterior part of the calvarium (figs. 53B and 54A). Its insertion is into the freely movable galea aponeurotica. A derivative of the pre-auricular muscle complex is the m. tragohelicinus, which has settled down on the ear cartilage, bridging the cleft between the tragus and the helix (figs. 53 A and 55C). In this form the m. tragohelicinus is commonly found in all primates except man, in whom this muscle is usually reduced to the vestigial m. tragicus, while another persisting portion of it gave rise to the m. helicis major, a very variable and inconstant element of the human ear musculature.

In the macaque little differentiation has taken place in the musculature of the midface region (figs. 53B and 54A). There, the powerful zygomaticus muscle mass has remained in broad connection with the well-developed m. orbicularis oculi, thus forming a m. zygomatico-orbitalis. A well defined portion of this muscle sheet has gained bony attachment to the zygomatic arch. But there is no differentiation as in man, particularly in the White race, into a caput zygomaticum of the m. quadratus labii superioris and a distinct m. zygomaticus. The m. nasolabialis—comprising the muscle material which in man is differentiated into the m. procerus nasi, the caput angulare of the m. quadratus labii inferioris and the exclusively human, yet very variable and inconstant vestiges known as mm. dilatatores narium ant. et post. and m. apicis nasi—forms in the rhesus macaque a continuous muscle plate which covers the whole nose and expands downward into the upper lip (fig. 53B). The bilateral anlagen of the m. nasolabialis have fused in the midline to build an unpaired muscle, which is continuous above with the m. frontalis (fig. 54A). In the supraciliary region the m. depressor supercilii (figs. 53B and 54A) may be recognized in primitive connection with the supra-orbital portion of the m. orbicularis oculi. Below, it passes over the ligamentum palpebrale mediale to become secondarily continuous with the muscle bundles of the infra-orbital portion of the m. orbicularis oculi. After removal of the m. depressor supercilii and the most medial bundles of the supra-orbital portion of the m. orbicularis oculi, the deeply situated m. corrugator supercilii becomes visible (fig. 54B). This muscle has bony origin in the glabellar region. From there it spreads in a fan-shaped fashion over the supra-orbital margin. Some of its medial bundles continue upward into the medial bundles of the m. frontalis, while some of its lateral bundles may be found continuous

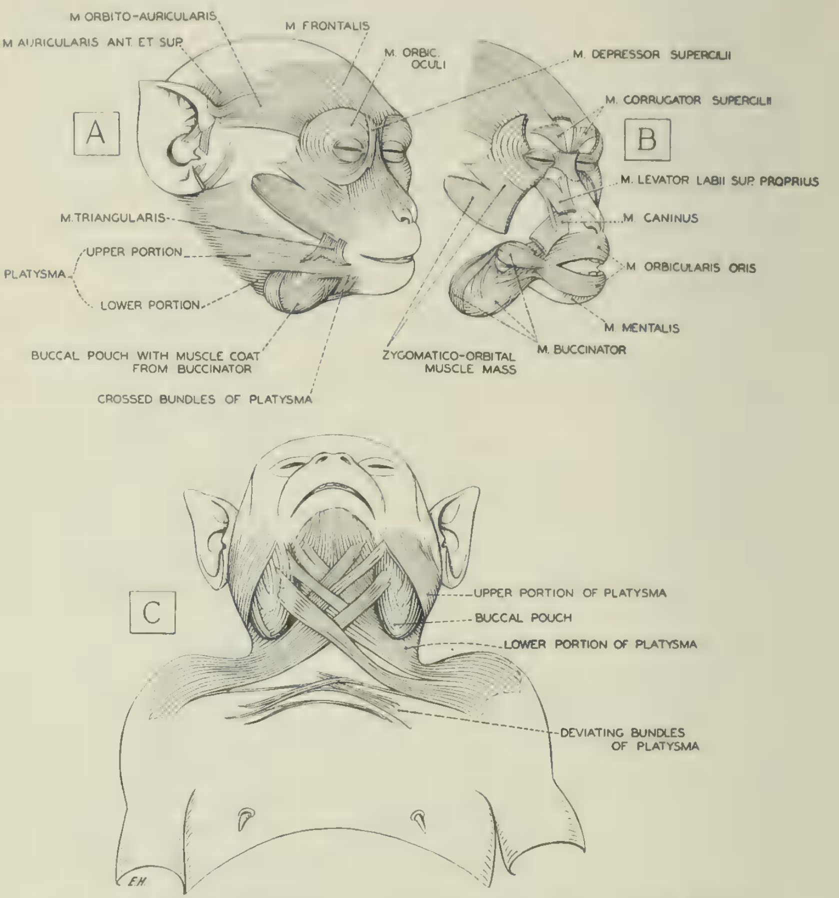
M ORBITO-AURICULARIS
M AURICULARIS ANT. ET SUP.
M FRONTALIS
M. ORBIC. OCULI
M. DEPRESSOR SUPERCILII
M. CORRUGATOR SUPERCILII
A
B
M. LEVATOR LABII SUP. PROPRIUS
M.TRIANGULARIS
M. CANINUS
PLATYSMA
UPPER PORTION
LOWER PORTION
M ORBICULARIS ORIS
M. MENTALIS
M. BUCCINATOR
BUCCAL POUCH WITH MUSCLE COAT FROM BUCCINATOR
ZYGOMATICO-ORBITAL MUSCLE MASS
CROSSED BUNDLES OF PLATYSMA
C
UPPER PORTION OF PLATYSMA
BUCCAL POUCH
LOWER PORTION OF PLATYSMA
DEVIATING BUNDLES OF PLATYSMA
E.H.

FIG. 54. The superficial facial musculature (continued). (Drawn by E. Huber.) A and B represent largely the derivatives of the sphincter colli profundus. In B part of the more superficial of these muscles have been cut away in order to expose the deeper ones. Emphasis is here laid on the orbicularis oris-buccinator system. Note in B that part of the m. buccinator forms the muscular coat of the buccal pouch which is herniated through the platysma plate, splitting this into an upper and a lower portion (compare A and C).

C, view from below to show the extent of the platysma plates of the two sides and their specializations in connection with the formation of the buccal pouches.

with deep bundles of the m. orbicularis oculi. The connection between the m. depressor supercilii and m. orbicularis oculi, and the connections between the m. corrugator supercilii, m. frontalis and m. orbicularis oculi in the supra-orbital region are primitive connections, while, on the other hand, the continuity of the m. frontalis with the m. nasolabialis represents a secondary fusion of supra-orbital with infra-orbital muscle entities established early in the phylogeny of the primates. All these muscles are derivatives of the pars pre-auricularis sph. colli profundi, as evidenced through comparative anatomical investigations on the lower primates (Huber 1931).

As regards the derivatives of the pars oris sph. colli profundi, these are likewise found on a comparatively simple plan in the rhesus monkey. One portion, the m. triangularis, has broken through the zygomaticus muscle mass and has spread out fanwise over an area lateral to the angle of the mouth (figs. 53B and 54A). Below, it secondarily overlaps the platysma. It has, however, not yet expanded as far as the lower border of the mandible, as it has in the anthropoid apes and man. Above, it continues into the well developed m. caninus (pars canina of the m. orbicularis oris), which has a broad origin from the maxilla. This becomes visible after removal of the overlapping insertional section of the zygomatico-orbital muscle mass (fig. 54B). In the macaque there is no m. risorius and no m. transversus menti; the former is a characteristic human structure while the latter also occurs occasionally in great anthropoid apes (compare Huber 1931, p. 59/60). The m. orbicularis oris forms a powerful coarse-fibered muscle which encircles the mouth cleft (fig. 54B). In the median line of both upper and lower lips a large mass of bundles of the m. orbicularis pass over without interruption to the opposite side, while at the corner of the mouth at least some of the marginal bundles remained uninterrupted. Laterally the bundles of the upper lip and lower lip portions of the m. orbicularis oris interlace and become continuous with the similarly coarse-fibered m. buccinator, which forms the muscular coat of the buccal wall (fig. 54B). The orbicularis oris and the buccinator thus form a morphological and functional unit. Additional deep bundles of the buccinator (not shown in figures) arise from the alveolar border of both upper and lower jaw, on the maxilla uninterruptedly from the posterior molar teeth as far forward as the first premolar tooth; on the mandible as far forward as the canine tooth, but with a large gap in the continuity of the linear origin in the region of the premolar teeth. The extent of this gap, however, varies (see also Lightoller 1928). In figure 2b it may be noted that a superficial bundle layer of the buccinator arising from the pterygomandibular ligament passes in a horizontal direction towards the mouth cleft, where it inserts into the "modiolus" at the corner of the mouth. At this point there also insert some muscle bundles from both the upper and lower lip portions of the m. orbicularis oris as well as bundles of the platysma, and a deep portion of the zygomaticus muscle mass which is intruded between the caninotriangularis (fig. 54, A and B) and buccinator muscles (fig. 54B). A large portion of the m. buccinator has become involved in the buccal pouch. It now covers the wall of the pouch in the manner as illustrated in fig. 54B. There are considerable individual variations in the details of arrangement of the buccinator portion relative to the buccal pouch; moreover, additional bundles from the platysma may reinforce the muscular wall of the pouch.

Owing to the strengthening of the muscular coat the pouch can be greatly distended. Food temporarily stored therein is repelled into the buccal cavity by voluntary contraction of the musculature of the pouch. However, when the pouch has been tightly packed with food and overdistended, the muscle coat of the pouch is not sufficiently strong to expel the food. Under such circumstances the animal pokes the food back into the buccal cavity with the aid of the fist.

While incisivi muscles—characteristic of the orbicularis oris-buccinator system of man—are not distinct in the rhesus macaque, a distinct m. mentalis (fig. 54B) is present. It arises on the mandible from the alveolar border in the region of the incisor teeth. Its bundles radiate to the skin over the chin. At its origin the m. mentalis remains in primitive connection with deep bundles of the buccinator. The m. levator labii superioris proprius (fig. 54B), the homologue of the caput infraorbitale m. quadrati labii superioris of man, on the other hand, has given up its connection with its matrix, the orbicularis oris-buccinator. It arises as a thin layer from the maxilla just below the infra-orbital margin under cover of the m. orbicularis oculi and m. nasolabialis (compare fig. 54B with figs. 54A and 53B). In its course downward it passes over the origin of the m. caninus and m. orbicularis oris to become inserted into the upper lip. In figure 54B the insertional portion of the levator labii superioris proprius is cut way to show the m. caninus in its relation to the upper lip portion of the m. orbicularis oris. Lastly, it may be mentioned that such nasal muscles as the pars transversa and pars alae nasi, and the m. depressor septi mobilis nasi, known from human anatomy, do not occur in the rhesus macaque.

THE N. FACIALIS

The superficial facial musculature is innervated exclusively by branches of the n. facialis. Immediately after its emergence from the stylomastoid foramen this nerve gives off the ramus auricularis posterior (fig. 55D), which, still under cover of the parotid gland, sweeps around the anterior border of the m. sternocleidomastoideus to continue its course occipitalward between the mastoid process and the ear (fig. 55A). It soon breaks up into a series of smaller branches which innervate the nuchal portion of the platysma and the entire postauriculo-occipital muscle group. The first twig coming off from the r. auricularis posterior enters the nuchal platysma. Another, smaller twig enters the m. antitragicus and the adjacent portion of the mm. obliqui et transversi. After having given off these two twigs the r. auricularis posterior divides into two branches. The first of these ascends to the occipital region to supply the m. occipitalis and m. auricularis posterior, as well as sections of the mm. obliqui et transversi, while the second branch (see also fig. 55B) ascends along the concha of the ear cartilage, thereby passing below the m. auricularis posterior. In its course it gives off a few small twigs to the mm. obliqui et transversi, others to the posterior section of the m. auricularis anterior et superior. Its terminal twig passes under the latter muscle and winds around the concha (fig. 55, A and B) to the anterior surface of the ear, where it ends in the m. helicis (fig. 55B).

The next branch given off from the stem of the n. facialis is the ramus digastricus (not shown in figures). It supplies the m. stylohyoideus and the posterior belly of the m. digastricus (see chapter VII).

The rest of the n. facialis breaks up into several larger branches which radiate under cover of the parotid gland (fig. 55D) and eventually appear at the outer contour of this structure. They spread out into the face to supply with their numerous twigs the various muscle complexes and individual muscles of the face, i.e. the mimetic muscles in the strict sense. Although the ramifications of these pre-auricular facial branches are subject to considerable individual variations, figure 55D nevertheless will give an adequate orientation: Here, the auriculo-temporo-frontal branch after a short course divides into two parts, the one (r. auricularis) ascending in front of the ear to ramify in the m. tragohelicinus and anterior section of the m. auricularis anterior et superior (see also fig. 55B), while the other larger branch, the r. supra-orbitalis (fig. 55D), gives off a whole series of twigs which enter the orbito-auricular muscle plate, m. frontalis, the supra-orbital portion of the m. orbicularis oculi and the mm. depressor and corrugator supercilii. Over the zygomatic arch a r. zygomatico-orbitalis branches off to supply the zygomaticus muscle mass and the adjacent part of the m. orbicularis oculi (fig. 55D).

There are two to three rami buccolabiales (fig. 55D), the middle one being the largest and most constant. These branches take a more horizontal course toward the cheek, where they break up into a series of

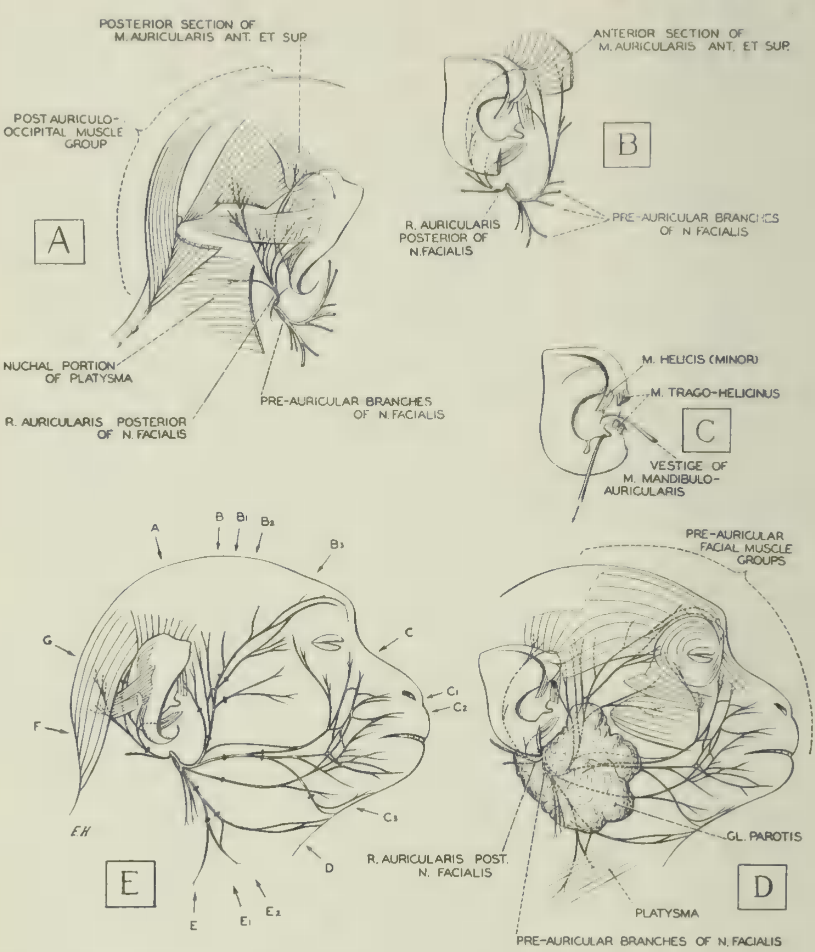
POSTERIOR SECTION OF M. AURICULARIS ANT. ET SUP.
POST AURICULO-OCCIPITAL MUSCLE GROUP
A
NUCHAL PORTION OF PLATYSMA
R. AURICULARIS POSTERIOR OF N. FACIALIS
PRE-AURICULAR BRANCHES OF N. FACIALIS
ANTERIOR SECTION OF M. AURICULARIS ANT. ET SUP.
B
R. AURICULARIS POSTERIOR OF N. FACIALIS
PRE-AURICULAR BRANCHES OF N FACIALIS
M. HELICIS (MINOR)
M. TRAGO-HELICINUS
C
VESTIGE OF M. MANDIBULO-AURICULARIS
A
B
B1
B2
B3
C
C1
C2
G
F
C3
E.H
D
E
E
E1
E2
PRE-AURICULAR FACIAL MUSCLE GROUPS
GL. PAROTIS
R. AURICULARIS POST. N. FACIALIS
D
PLATYSMA
PRE-AURICULAR BRANCHES OF N. FACIALIS

FIG. 55. The n. facialis. (Drawn by E. Huber.) A and B, innervation of the post-auriculo-occipital muscle group in contrast to the pre-auricular muscle territory (B). C, a rare variation, vestige of the m. mandibulo-auricularis, in close genetic relation to the m. helicis (minor), both being muscles of the postauricular group. D, the peripheral branches of the n. facialis, their topographic relation to the parotid gland, and their distribution to the superficial facial musculature. In order not to complicate the illustration, only a few of these muscles are lightly indicated (compare respective muscles in figs. 53 B and 54, A, B, C). E, the distribution of the peripheral, pre- and postauricular facial branches with the points (a–g) marked where these branches can best be stimulated with the electrode in order to unravel their exact distribution within the muscle complexes and individual facial muscles, and to gain additional information about the actions of these muscles.

smaller twigs which in turn ramify, forming a very complex network. From this buccal plexus a good-sized branch ascends anteriorly to the zygomatic arch to supply the lateral and infra-orbital portions of the m. orbicularis oculi, while another branch descends to the margin of the mandible and along this oralward to supply the muscles over the chin, i.e. the under lip portion of the platysma, the m. mentalis and portions of the m. orbicularis oris, while the rest of the numerous branches of the buccal plexus ramify within the m. nasolabialis, m. levator labii superioris proprius and the orbicularis oris-buccinator complex.

Lastly there is a large branch (r. colli), which descends to the angle of the mandible (fig. 55D). There it divides into two main branches which are usually connected by a small anastomosis. The anterior of these two branches follows the mandible to ramify in the muscles of the chin region, while the posterior branch enters the caudal section of the platysma. In addition, there are several smaller branches which pierce the parotid gland separately (fig. 55D) to ramify in the adjacent portion of the platysma.

A series of twigs of the various cutaneous branches of the n. trigeminus (not shown in figures) join the pre-auricular facial branches, thus adding to the complexity of the facial plexus. These trigeminal-facial anastomoses are most numerous in the network of the rami buccales. While experiments have revealed that these trigeminal anastomoses, like those branches of the cervical plexus which enter into anastomosis with the facial nerve, do not contribute motor elements for the facial musculature, the significance of these anastomoses is not yet clearly understood. Most probably they are merely the result of a close topographical relationship of functionally distinct nerve elements.

Owing to the rich ramification and plexus formation of the n. facialis it is impossible to determine by purely morphological method of investigation the exact distribution of the terminal twigs within the various muscle complexes and individual facial muscles. The only satisfactory approach therefore is the experimental method, i.e. electrical stimulation in the anesthetized animal of the individual facial branches at such points (a–g) as those marked in figure 55E, and observation of the contraction resulting in the corresponding exposed muscle groups. The compound muscle contractions hereby obtained suggest characteristic features of facial expression as observed in the conscious rhesus macaque.

The rôle played by the superficial facial musculature of the rhesus macaque in *facial expression*, is brought forth through grimace-like group actions of facial muscles. Most characteristic in the macaque is the bilaterally synergic contraction of the old phylogenetic unit comprising the mm. auricularis posterior and occipitalis, which results in pulling backward the scalp and simultaneous retraction of both ears. The ears may, however, be moved separately, and single portions of the ear are often seen in play. Within the musculature of the face proper, the m. orbicularis oculi naturally plays an important rôle. Very vivid, on the other hand, is the synergic contraction of the powerful zygomaticus muscle mass, m. nasolabialis and platysma. In general, it may be noticed that the range of individual features of facial expression in the macaque, as well as in the other lower catarrhines and in the platyrrhines, is comparatively small, and all these expressions are still largely stereotypical. (For comparison of facial expression in the anthropoid apes and man see Huber 1931, and further literature contained therein.)

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Chapter IX

NASAL CAVITY, LARYNX, MOUTH AND PHARYNX

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THE NOSE

(Figs. 56, 57)

The nasal cavity, the most cephalic of the subdivisions of the respiratory system, extends from the external nasal orifices, through which it opens to the exterior of the body, to the internal nasal orifices or choanae which connect it with the nasopharynx.

The nasal cavity of the monkey differs from that of man in four fundamental respects, namely, the absence of frontal, ethmoidal, and sphenoidal sinuses; the absence of a homologue of the human superior nasal concha; the existence of a direct communication with the oral cavity through the incisive foramina; and the presence of a membranous partition continuous with the dorsal border of the bony septum.

The cavity is lined throughout with mucous membrane which is continuous with that of the nasopharynx, with the skin at the external nasal orifices, with the mucous membrane of the palate at the incisive foramina, and which extends into and lines the walls of the maxillary sinuses.

External nose

The external nose is flattened, and is covered on its external surface with hairy skin. The skeletal framework comprises the ventral part of the *septal cartilage*, which supports the nose in the median plane, and on either side, a somewhat triangular plate of cartilage in the wing of the nose, the *alar cartilage*. The caudal border of this cartilaginous plate, the shortest of the three, lies in the margin of the external nasal orifice. The lateral border is slightly concave, the medial border is convex. The *apex* is rounded and falls short of reaching the bony margin of the external nasal opening.

Nasal cavity

In sagittal section, the nasal cavity is essentially triangular in shape, and is subdivided into right and left symmetrical halves by the nasal septum.

The cranial wall is short and narrow and consists of the cribriform plate of the ethmoid bone, through the foramina of which pass the filaments of the olfactory nerve from the nasal cavity to the anterior cranial fossa. The dorsocranial wall is covered by mucous membrane on the ventral surface of the body of the sphenoid bone. This wall presents nothing of special interest. There is no sphenoidal sinus and, therefore, no ostium. The caudal wall consists of the mucous membrane covering the bones of the palate. The lateral wall (fig. 56) is made up of the following bones: nasal, premaxilla, maxilla, lacrimal, ethmoid, frontal, palatine, and inferior nasal concha. The details of structure and relationships of these several bony elements will not be undertaken here, and the lateral nasal wall is described with the mucous membrane in situ. This wall is irregular, being marked by two prominent projections of bone covered with mucous membrane, the *nasal conchae*, which correspond in position and relationships to the middle and the inferior conchae of man, respectively. There is nothing comparable to the human supe-

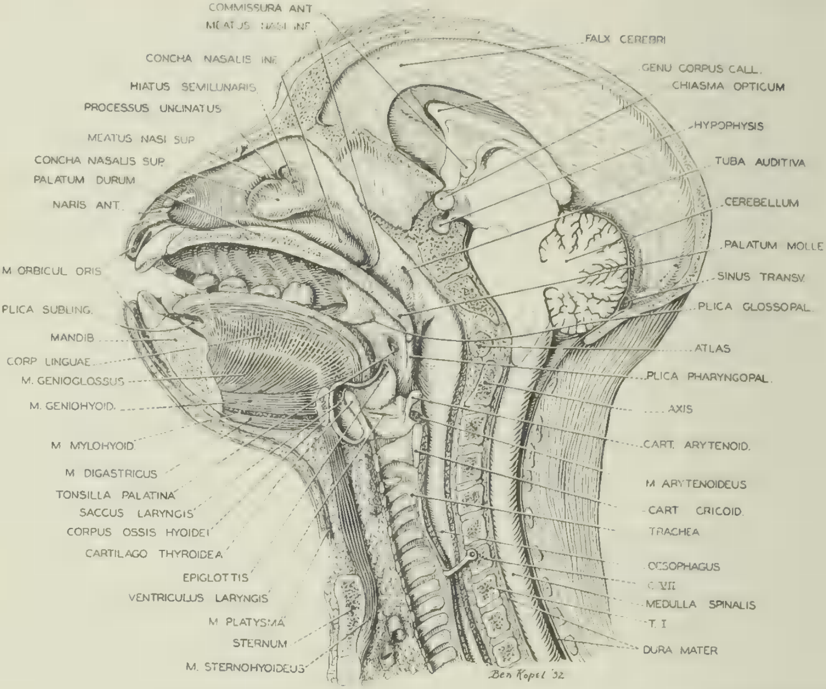

Fig. 56. Sagittal section of the head and neck slightly to the right of the median plane.

rior concha, this part of the wall being smooth and not appreciably elevated.

The *superior concha* is a tongue-shaped piece of bone whose dorsal extremity is attached to the dorsal part of the lateral nasal wall. Its cranial, caudal, and ventral margins are free. Just above the concha is a slight depression simulating the human superior meatus, and caudal to it is a depression corresponding in position to the human middle meatus. As the cranial border of the concha is unattached, these meatuses are continuous.

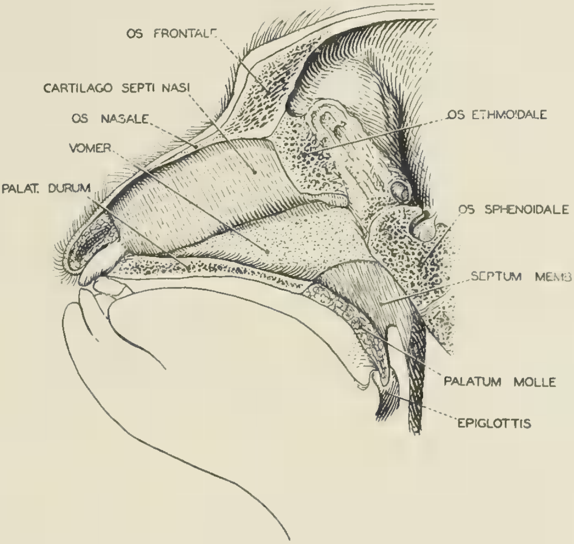

Fig. 57. The nasal septum.

The *inferior concha* is expanded in its ventral part and blends insensibly with the adjacent part of the wall. On its cranial aspect, however, there is a prominent nipple-like process containing cartilage which underlies the wing of the nose and which is continuous with the lateral border of the cartilaginous plate in the wing. The dorsal extremity of the inferior concha extends a little beyond the dorsal border of the hard palate.

If the superior concha be removed, there is uncovered a prominent *uncinate process*, dorsal to which is a curved depression, the *semilunar hiatus*, into which the maxillary sinus opens. The caudal extremity of the nasolacrimal duct opens into the *inferior meatus* under cover of the ventral part of the inferior concha.

The medial wall or *nasal septum* (fig. 57) is cartilaginous, bony, and membranous. The *septal cartilage* is an irregularly quadrilateral plate having ventrocaudal, ventrocranial, dorsocaudal, and dorsocranial borders. The ventrocaudal border is attached to the premaxillae and to the soft parts between the external nasal orifices and the upper lip. The ventrocranial border, in its upper part, attaches to the nasal bones, and in its caudal portion, to the soft parts of the external nose. The dorsocaudal border attaches to the vomer bone, while the dorsocranial border articulates with the perpendicular plate of the ethmoid. The osseous elements of the nasal septum are the perpendicular plate of the ethmoid bone and the vomer. The former occupies the cranial and dorsal part of the septum, the latter forms the caudal and dorsal part. The *membranous part* of the septum properly belongs with the nasopharynx but will be described at this point. It is a sheet of connective tissue, lined by nasal epithelium, which attaches to the dorsal border of the vomer, to the cranial surface of the soft palate, and to the dorsal wall of the nasopharynx ventral to the body of the sphenoid and the basilar part of the occipital bone.

NERVES AND VESSELS. The nerves of the nasal cavity are the olfactory, the ethmoidal, the lateral nasal, and the medial nasal or nasopalatine.

The *olfactory nerve* consists of numerous bundles of fibers which ramify in the mucous membrane over the cranial and dorsal part of the lateral wall and the septum. On the lateral wall they extend on the upper concha. On the septum they correspond in distribution essentially to the area of the perpendicular plate of the ethmoid bone; they do, however, extend a little beyond it and on the cartilaginous part.

The *ethmoidal nerve* enters the nasal cavity through the ventral part of the cribriform plate of the ethmoid, and is distributed to the walls of the ventral part of the nasal cavity.

The *lateral nasal nerves* enter the nasal cavity through the sphenopalatine foramen and ramify over the lateral wall.

The *medial nasal nerve* passes dorsoventrally on the vomer bone, through the incisive foramen, and terminates within the tuft of mucous membrane in this location.

Vessels accompany the ethmoidal, lateral nasal, and medial nasal nerves.

THE LARYNX

(Figs. 56, 58, 59)

The larynx is that part of the respiratory system connecting the laryngeal pharynx cranially with the trachea caudally. It lies ventral to the vertebral column and consists of a skeletal framework of cartilages, ligaments, and membranes. Associated with it is a group of striated muscles which act upon the skeletal elements and which are utilized in the production of the sounds of different pitch which the animal is capable of making.

The larynx of the monkey occupies a relatively high position in the neck, a considerable part of the trachea being cranial to the superior border of the sternum. When the head is in the anatomical position corresponding to that of man, with the face directed forward, the caudal border of the cricoid cartilage is on a level with the cranial part of the body of the fourth cervical vertebra, and the hyoid bone lies ventral to the caudal part of the body of the epistropheus.

Laryngeal cavity

(Fig. 56)

The cavity of the larynx is irregular in shape and consists of three dilated portions which are incompletely separated from one another by two projections from each lateral wall, the *ventricular fold* or false vocal cord, and the *vocal fold* or true vocal cord. In a craniocaudal direction the divisions of the cavity are the vestibule, the ventricle, and the caudal compartment. The *vestibule* extends from the aditus, or cranial opening of the larynx, to the ventricular fold; the *ventricle* is the lateral diverticulum between the ventricular fold and the vocal fold; and the *caudal compartment* extends from the vocal fold to the caudal border of the cricoid cartilage, where it becomes continuous with the lumen of the trachea.

The *aditus* (fig. 59), the opening from the laryngopharynx into the vestibule of the larynx, is bounded ventrally by the dorsal surface of the epiglottis, and laterally, by two prominent elevations of mucous membrane containing the cranial extremities of the arytenoid and cuneiform cartilages, respectively. These two elevations or tubercles are at the same level and there is no definite aryepiglottic fold. The ventral tubercle is the smaller and is rounded; the dorsal tubercle is pyriform, the part corresponding to the stem of the pear meeting with that of the tubercle of the opposite side. The ventral tubercle lies dorsomedial to and near the lateral edge of the epiglottis.

Ventral to the thyroid cartilage, and between it and the hyoid bone, is a relatively large *laryngeal sac* which communicates with the cavity of the vestibule by a constricted opening in the median line through the caudal part of the epiglottis slightly cranial to the ventricular folds

The sac is lined by mucous membrane continuous with that of the larynx.

Skeletal framework of the larynx

(Figs. 56, 58, 59)

The skeletal framework of the larynx consists of the *hyoid bone* and a number of *cartilages*, *membranes*, and *ligaments*. The cartilages are paired and unpaired. The paired cartilages are the arytenoid and the cuneiform, the unpaired cartilages are the thyroid, the cricoid, and the epiglottis.

The *hyoid bone* consists of a ventral, median part, the *body*, and two dorsal projections on each side, the *greater cornua* and the *lesser cornua* (fig. 58A). The body is a thin shell of bone which on its dorsal surface presents a deep concavity lodging the laryngeal sac. The caudal part of the body of the bone extends over the thyroid cartilage in the median line to about midway between the cranial and caudal borders of the cartilage. The lesser cornu is attached to the skull by means of the stylohyoid ligament. The greater cornu is connected with the cranial border of the thyroid cartilage by the thyrohyoid membrane.

The *thyroid cartilage* is shield-shaped and consists primarily of two laminae which are continuous across the median line ventrally in a more or less rounded manner. Each *lamina* has a cranial, a caudal and a dorsal border. At the junction of the cranial and dorsal borders is the *cranial cornu*, to which is attached the dorsal part of the thyrohyoid membrane. Just ventral to the cranial cornu is a notch for the vessels and nerve which pass through the thyrohyoid membrane. At the junction of the dorsal and caudal borders is the *caudal cornu*, which bears an articular facet for articulation with the cricoid cartilage.

The *cricoid cartilage* is essentially quadrilateral in cross section. The dorsal part or *lamina* is marked on its dorsal surface by a prominent vertical crest between the fossae from which arise the fibers of the dorsal crico-arytenoid muscle. On the lateral part of the cranial border of the lamina is an articular facet for the arytenoid cartilage. On the lateral part of the lamina near the caudal border is a facet for the caudal cornu of the thyroid cartilage (fig. 58, B and C). The remainder of the cricoid cartilage, that is, exclusive of the lamina, is the *arch*.

The *epiglottis* is a tongue-shaped plate of cartilage situated dorsal to the body of the hyoid bone and the cranial part of the thyroid cartilage. It is attached to the dorsal surface of the body of the hyoid bone by the *hyo-epiglottic ligament*, to the tongue by the *glosso-epiglottic ligament*, and by its caudal, pointed extremity to the thyroid cartilage. The mucous membrane on its oral surface is continuous with that of the tongue.

The *arytenoid cartilages* surmount the cranial border of the lamina of the cricoid cartilage. Each arytenoid cartilage has a *body* from which there project three prominent processes. The *cranial process* is long, slender, and expanded at its apex. A distinct corniculate cartilage does not exist. The cartilage of the apices of the arytenoids is continuous across the median line. The *muscular process* projects laterally from the caudal part of the body and to it are attached some of the intrinsic muscles of the larynx. The *ventral process* lies imbedded within the conus elasticus some distance caudal to the vocal fold and relatively near the cranial border of the cricoid cartilage. The caudal surface of the body and of the muscular process have an articular facet for the crico-arytenoid joint.

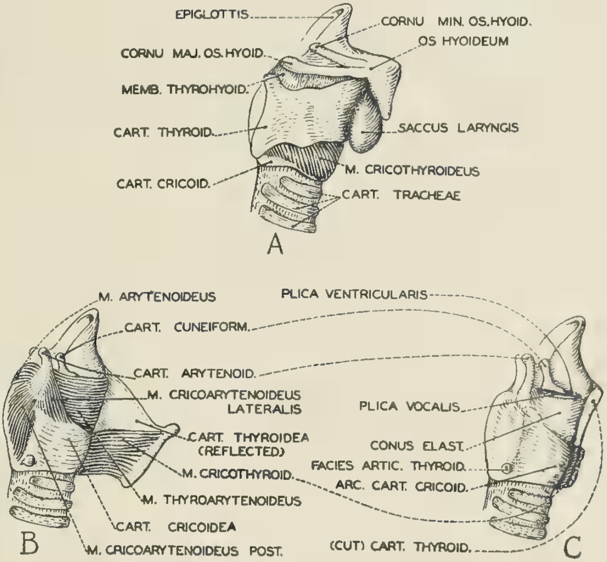

FIG. 58. The larynx. A, right lateral aspect. B, the intrinsic muscles. C, the skeletal elements (muscles removed).

The *cuneiform cartilages* are L-shaped structures, smaller than the arytenoids, which lie ventral to the rostral part of the cranial processes of the arytenoids and imbedded within the substance of the lateral laryngeal wall. The *cranial process* lies parallel to the cranial process of the arytenoid cartilage; the *ventral process* lies within the ventricular fold and extends ventrally for a considerable distance.

The *diarthrodial articulations* of the larynx are the cricothyroid and the crico-arytenoid. The *cricothyroid joint* permits of movement by which the ventral parts of the thyroid and cricoid cartilages may be approximated, thus increasing the tension of the vocal folds. The *crico-arytenoid joint* permits of movement in two ways. The two arytenoid cartilages may be approximated by the action of the arytenoid muscle, and the arytenoid cartilage may rotate so that the ventral process may move laterally and medially, thus altering the size of the *glottis* or space between the vocal folds. Inasmuch as the apices of the arytenoid cartilages are connected by cartilage across the midline, the lateral movement of the arytenoid as a whole is necessarily limited.

The *ventricular folds*, or false vocal cords, are one on either side of the midline and constitute the boundary between the vestibule and the ventricle. Each ventricular fold is a band of connective tissue which attaches ventrally to the dorsal surface of the thyroid lamina just lateral to the midline. Dorsally, it attaches to the cranial process of the arytenoid cartilage. Within it is the ventral process of the cuneiform cartilage.

The *vocal folds*, or true vocal cords, are likewise paired structures, each having a relatively sharp free edge projecting into the laryngeal cavity between the ventricle and the caudal compartment. The vocal fold is a band of connective tissue which attaches ventrally to the dorsal surface of the thyroid lamina caudal to the ventral attachment of the ventricular fold. Dorsally, it attaches to the cranial process of the arytenoid cartilage at approximately its middle. The ventral process of the arytenoid cartilage is considerably caudal to the vocal fold and is imbedded within the conus elasticus.

The membranes of the larynx are connective tissue sheets which occupy the intervals between the cartilaginous and bony elements. These membranes are the thyrohyoid, cricothyroid, conus elasticus and cricotracheal. The *thyrohyoid membrane* attaches the cranial border of the thyroid cartilage to the greater cornu of the hyoid bone. It is penetrated by the superior laryngeal vessels and the internal branch of the superior laryngeal nerve. The *cricothyroid membrane* is a prominent band of tissue which connects the ventral part of the cricoid cartilage with the caudal border of the thyroid cartilage in, and on either side of, the median line. Laterally, this membrane becomes continuous with the *conus elasticus*, which lies between the thyro-arytenoid muscle and the mucous membrane of the larynx. Ventrally, it is attached to the dorsal surface of the lamina of the thyroid cartilage medial to the origin of the thyro-arytenoid muscle; caudally, it attaches along the cranial border of the cricoid cartilage ventral to the lamina; dorsally, it is applied to the ventral surface of the arytenoid cartilage; and cranially, it becomes continuous with the vocal fold and the lateral wall of the ventricle of the larynx. The *cricotracheal membrane* connects the caudal border of the cricoid cartilage with the first ring of the trachea.

Intrinsic muscles of the larynx

(Fig. 58)

The movements of the cartilages of the larynx upon one another are produced by a group of *striated muscles* called the intrinsic muscles of the larynx. These muscles are four pairs, the cricothyroids, dorsal crico-arytenoids, lateral crico-arytenoids, thyro-arytenoids, and the unpaired arytenoid muscle.

The *cricothyroid muscle* (m. cricothyroideus) arises from the external surface of the lateral part of the cricoid cartilage. Its more ventral fibers pass cranially and dorsally at an angle of about 45°; the dorsal fibers do so at an angle of about 30°. Fibers of both parts of the muscle insert on the caudal border of the lamina of the thyroid cartilage and are continued on the medial surface of the lamina to within a short distance of the cranial border. The two cricothyroid muscles, at their origins, almost meet in the median line, but between their insertions there is a considerable interval which contains the ventral part of the cricothyroid membrane. When the muscle contracts, the ventral parts of the thyroid and cricoid cartilages are approximated, the arytenoid cartilages are tipped dorsally, and the tension of the vocal fold is increased. The muscle is *supplied by the external branch of the superior laryngeal nerve.*

The *dorsal crico-arytenoid muscle* (m. crico-arytenoideus posterior) arises from the dorsal surface of the lamina of the cricoid cartilage. The fibers converge as they pass cranially and laterally and insert on the dorsal surface of the muscular process of the arytenoid cartilage. When the muscle contracts, the muscular process is pulled dorsally, the ventral process moves laterally, and the transverse diameter of the glottis is increased. The muscle is *supplied by the inferior laryngeal nerve.*

The *lateral crico-arytenoid muscle* (m. crico-arytenoideus lateralis) is a triangular mass which arises from the dorsal one-half of the cranial border of the lateral part of the cricoid cartilage. It inserts on the ventral surface of the muscular process of the arytenoid cartilage. When the muscle contracts the muscular process is pulled ventrally, the ventral process moves medially, and the glottis is narrowed, antagonizing the action of the dorsal crico-arytenoid. The lateral crico-arytenoid muscle is *supplied by the inferior laryngeal nerve.*

The *thyro-arytenoid muscle* (m. thyro-arytenoideus) is a relatively large, thick muscle which arises from the dorsal surface of the lamina of the thyroid cartilage just lateral to the median line. The fibers pass dorsally and converge to insert on the ventral surface of the caudal part of the arytenoid cartilage medial to the muscular process. The medial surface of the muscle lies against the conus elasticus but is easily separated from it. When the muscle contracts, the arytenoid cartilages are moved ventrally together with the cranial part of the cricoid lamina and the tension of the vocal folds is decreased. The muscle is the antagonist of the cricothyroid. It is *supplied by the inferior laryngeal nerve.*

The *arytenoid muscle* (m. arytenoideus) consists of a bundle of transverse fibers extending from the dorsal surface of one arytenoid cartilage to that of the other. A considerable portion of the muscle attaches to the connective tissue between the larynx and the laryngopharynx. There is no oblique portion of this muscle, and consequently, no aryepiglottic muscle. Just how the muscle acts is somewhat questionable. As the cartilage of the apices of the arytenoids is continuous across the median line there can be but little lateral movement of the entire arytenoid on the cricoid. Because of its dorsal attachment to the arytenoid cartilages, it is possible that it may assist the dorsal crico-arytenoids in widening the glottis. The muscle is *supplied by the inferior laryngeal nerve.*

Nerve and vessels of the larynx

The *superior laryngeal nerve* sends two branches to the larynx, the external and the internal. The former supplies the cricothyroid muscle, the latter passes through the thyrohyoid membrane to supply the mucosa. The *inferior laryngeal nerve* passes into the larynx under cover of the caudal border of the inferior constrictor muscle of the pharynx where it breaks up into branches for supply of the muscles.

The *superior laryngeal vessels*, which are the principal source of supply and drainage of the larynx, accompany the internal branch of the superior laryngeal nerve. The *inferior laryngeal artery* is apparently quite variable. In a gross dissection of one specimen it was present and accompanying the inferior laryngeal nerve. In another specimen it could not be identified. In a series of stained sections of another animal there was no artery of conspicuous size accompanying the inferior laryngeal nerve.

THE MOUTH

(Figs. 56, 59, 60)

The buccal cavity

(Fig. 56)

The mouth extends from the *rima oris* externally to the *faucial isthmus* internally, through which it becomes continuous with the oropharynx. The mouth cavity consists of two parts, the vestibule and the oral cavity proper. The *vestibule* is the part of the oral cavity which is limited externally by the lips and the cheeks, and internally by the teeth and the alveolar margins of the maxillae, the premaxillae, and the mandible. The *oral cavity* proper is bounded cranially by the hard and the soft palate; laterally and ventrally by the teeth and the alveolar margins; caudally by the tongue and the mucous membrane reflected from it to the mandible; and dorsally by the faucial isthmus. The oral cavity is lined throughout, excepting the teeth, by mucous membrane which is continuous dorsally with that of the pharynx, and ventrally with the skin at the rima oris. It also extends into and lines the cavity of the buccal pouch. Into the vestibule there open the ducts of the parotid glands, and the buccal pouch which serves for the accumulation of food preparatory to its mastication.

Buccal pouch

(Figs. 53, 54)

In the collapsed and fixed condition the buccal pouch extends about one-half inch below the caudal border of the body of the mandible. It presents a medial surface, a lateral surface, a ventral border and a dorsal border, which borders are continuous caudally in a rounded, U-shaped manner. The line of the ventral border of the pouch is slightly dorsal to the angle of the mouth, while the dorsal border crosses the angle of the mandible and overlies, in turn, the fibers of the platysma and the ventral fibers of the masseter muscles.

The pouch lies immediately beneath the skin and is loosely held to the subjacent structures by an investment of cervical fascia. As the platysma muscle passes from the neck to the face, its more ventral fibers pass deep to the pouch, a few inserting into its medial surface. The dorsal fibers of the platysma pass superficial to the pouch and are closely applied to it as they approach the angle of the mouth. The relations of the buccinator muscle to the pouch are somewhat complicated. The main mass of the muscle lies cranial to the opening of the pouch as its fibers pass ventrally to the angle of the mouth; the caudal fibers pass ventrally and insert along the dorsal border and on the medial surface of the pouch. There are a few fibers from the alveolar border of the mandible near its junction with the ventral border of the ramus passing to insert on the deep surface of the pouch (compare chapter VIII). The medial surface of the pouch, at its opening into the mouth, is held to the alveolar margin of the mandible by connective tissue and mucous membrane. The wall of the pouch contains interlacing bundles of striated muscle fibers. The opening of the pouch into the vestibule of the mouth is sufficiently large to admit the finger tip. The buccinator nerve sends fibers to the dorsal border of the pouch, and the facial and mental nerves supply its deep surface.

Salivary glands

The principal salivary glands are three pairs, the parotid, the submaxillary, and the sublingual.

The *parotid gland*, the largest of the three chief salivary glands, is situated caudal and ventral to the external ear, a small extension of it, however, lying dorsal to the cartilaginous external acoustic meatus. The cranial border of the gland lies along the caudal border of the zygoma; the gland extends caudalward to the angle of the mandible. The *parotid duct* emerges from the substance of the gland on its deep surface near the junction of the ventral border with the cranial border somewhat caudal to the zygoma and passes ventrally. On its way to the mouth it lies on the masseter muscle, at the ventral border of which it passes through the buccinator muscle to enter the vestibule opposite the first upper molar tooth. As it leaves the substance of the gland, the duct is covered superficially by a ventral extension of glandular tissue to the ventral border of the masseter muscle. This part of the gland pours its secretion dorsally and is drained by a small duct which enters the main duct.

The gland is covered by an extension of cervical fascia, superimposed upon which is the superficial muscular sheet of the neck and the skin. The external jugular vein emerges from its caudal border, and the great auricular nerve enters it dorsal to the vein.

The deep portion of the gland is wedge-shaped, having a ventromedial and a dorsomedial surface. The former is in relation with the masseter and the internal pterygoid muscles; the latter is, for the most part, in relation with the external surface of the sternocleidomastoid, digastric, and stylohyoid muscles, the internal carotid artery, the internal jugular vein, and the accompanying nerves. The gland may be readily separated from the sternocleidomastoid muscle, and, in the interval between them, the facial nerve located and traced to the stylomastoid foramen. The medial border of the gland, where the ventromedial and dorsomedial surfaces meet, lies between the stylomandibular ligament and the internal pterygoid muscle. The external carotid artery enters the gland on its dorsomedial surface and is crossed superficially by the branches of the facial nerve within the gland.

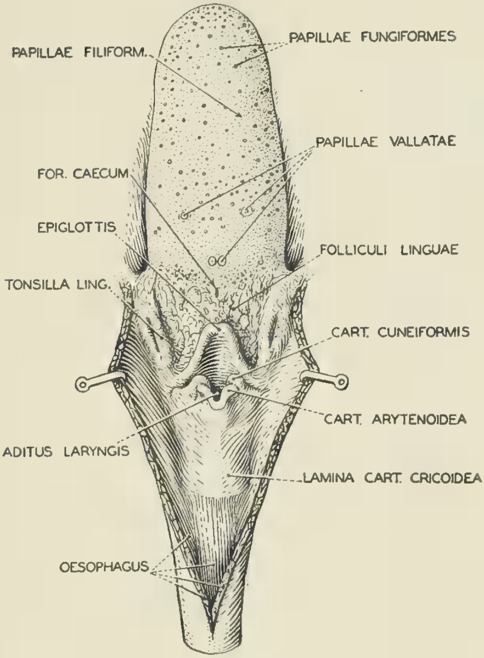

FIG. 59. The dorsal surface of the tongue and the larynx.

The *submaxillary gland*, which is considerably smaller than the parotid, and which is encapsulated by cervical fascia, lies immediately caudal and medial to the angle of the mandible. It is covered superficially by the platysma muscle and the skin, and in its cranial part by the angle of the mandible. Its dorsal border is in relation with the ventral border of the sternocleidomastoid muscle. The deep surface of the gland lies against the mylohyoid, thyrohyoid, sternothyroid, stylohyoid and posterior belly of the digastric muscles, the hypoglossal nerve, and the great vessels of the neck. The *submaxillary duct*, accompanied by an extension of glandular tissue, emerges from the cranial edge of the gland, passes immediately cranial to the tendon of the digastric muscle, then deep to the dorsal border of the mylohyoid muscle. It then runs along the deep surface of the sublingual gland, within which it is imbedded, and finally opens into the mouth on the cranial edge of a tuft of mucous membrane beneath the tongue. As the duct passes deep to the sublingual gland it is crossed superficially by the lingual nerve at the dorsal extremity of the gland. The external maxillary artery, which lies deep to the submaxillary gland, sends branches to it.

The *sublingual gland*, the smallest of the three chief salivary glands, is an elongated structure which lies just deep to the mucous membrane of the mouth, between the mylohyoid muscle and the side of the tongue. Its caudal border is in contact with and parallels the lateral edge of the geniohyoid muscle. The cranial border of the gland lies immediately beneath the oral mucosa and from it there emerge about twelve minute *sublingual ducts* which open into the mouth. The gland does not have a main duct. The gland extends dorsally almost to the dorsal border of the mylohyoid muscle. Its deep surface is in relation with the genioglossus and hyoglossus muscles, the hypoglossal and lingual nerves, and the sumaxillary duct which is imbedded within it. At the dorsal extremity of the gland the lingual nerve, the submaxillary duct, and the hypoglossal nerve lie close together and in this order in a craniocaudal direction.

PALATE

(Fig. 56)

The palate, which constitutes the cranial wall or boundary of the oral cavity proper, consists of a ventral part, the *hard palate*, comprising the palatine processes of the maxillae and the premaxillae, and the horizontal plates of the palatine bones; and a dorsal, movable part, the *soft palate*, consisting essentially of striated muscle, glands, and connective tissue. The palate is lined by mucous membrane, which, on the hard palate, is elevated in the form of eight or nine *transverse ridges*. On either side of the median plane, each of these ridges is concave dorsally, and the corresponding ridges of the two sides meet in the midline at a point which is directed dorsally. In the depressions between the ridges of the dorsal one-half of the hard palate may be seen grossly the relatively large ostia of the *palatal gland ducts*. On the ventral part of the hard palate, in the median line and just dorsal to the incisor teeth, is a triangular elevation of mucous membrane, whose apex is directed ventrally, on either side of which is a small aperture leading into the nasal cavity through the *incisive foramen.*

The *soft palate* is interposed between the dorsal part of the oral cavity, ventrally, and the dorsal part of the nasal cavity and the nasopharynx, dorsally. It is attached to the dorsal border of the hard palate, its caudal border is free, and extending from it in the median line is the *uvula.* The dorsal surface of the soft palate, which faces the nasopharynx, affords attachment for the caudal part of the membranous nasal septum. Extending from the oral surface of the lateral part of the soft palate to the side of the tongue and forming the lateral boundary of the faucial isthmus is the *glossopalatine fold*, within which are the fibers of the glossopalatine muscle. Dorsal to this fold is a depression, the tonsillar fossa, containing the *palatine tonsil*, and dorsal to this is a less pronounced fold of mucous membrane, the *pharyngopalatine fold*, containing the fibers of the pharyngopalatine muscle. The oral one-half of the substance of the soft palate is glandular and is sharply demarcated from the nasal one-half, which is muscular. The central part of the uvula is highly glandular and is surrounded by the sparse fibers of the uvular muscle.

Muscles of the soft palate

(Fig. 60)

Associated with and acting upon the soft palate are four pairs of striated muscles, the levator veli palatini, tensor veli palatini, glossopalatinus, pharyngopalatinus, and one unpaired, the musculus uvulae.

The *levator veli palatini muscle* arises by a somewhat pointed, fleshy, origin from the ventral surface of the petrous part of the temporal bone just caudal to the bony opening of the auditory tube, from the cartilaginous part of the auditory tube where it enters the bone, and by a few fibers which are blended with this part of the origin of the tensor veli palatini muscle. From its pointed or cylindrical origin, which is medial to that of the tensor, it flattens out as it descends in a ventromedial direction to insert into the dorsal part of the soft palate. As the fibers are followed into the palate they retain their individuality practically to the median line and blend with the muscular tissue of the uvula. When the muscle contracts, the soft palate is elevated and the cavity of the nasopharynx is closed off from the oropharynx.

The *tensor veli palatini muscle* at its origin is thin and flat. It arises from a linear attachment along the ridge of bone on the sphenoid between the pterygoid fossa and the temporosphenoidal synchondrosis, from the lateral surface of the cartilaginous portion of the auditory tube, and to a slight extent from the caudal surface of the petrous portion of the temporal bone dorsal to the tubal canal. The muscle passes ventrally and somewhat caudally, becomes tendinous and constricted, passes around the pterygoid hamulus, and inserts into the dorsal part of the soft palate just in back of the hard palate. When the muscle contracts it spreads and makes tense the soft palate.

The *glossopalatine muscle* is a distinct band of fibers occupying the glossopalatine fold and extending from the lateral part of the soft palate to the side of the tongue. When the muscle contracts it serves to approximate the tongue and the soft palate and to constrict the faucial isthmus.

The *pharyngopalatine muscle* occupies the pharyngopalatine fold and extends from the soft palate to the pharynx. Within the palate, the fibers are spread out and lie ventral to those of the levator. As the fibers pass from the palate to the pharyngopalatine fold they become concentrated into a slender bundle which passes caudally and blends with the musculature of the wall of the pharynx. The muscle serves to depress the soft palate and to constrict the space between the two pharyngopalatine folds.

The *uvular muscle* consists of a relatively thin shell of fibers which are directed ventrodorsally within the uvula and surrounding the cluster of glands forming the core of that structure. As the fibers of the muscle are followed ventrally they become scattered within the substance of the palate, and few, if any, attain the dorsal border of the hard palate. When the muscle contracts it shortens the uvula.

Nerves and vessels of the palate

The hard palate receives nerves and vessels which enter its substance through the incisive foramen, the terminal parts of the nasopalatine nerves and vessels; and through the posterior palatine foramina, the posterior palatine nerves and vessels.

The *tensor veli palatini* muscle is supplied by a branch of the *mandibular division of the trigeminal nerve.* The detailed innervation of the other palatal muscles has not been determined.

TONGUE

(Figs. 59, 60)

For descriptive purposes the tongue may be considered as consisting of a ventral three-fourths and a dorsal one-fourth, the former comprising that portion ventral to the *foramen caecum*, the latter, that part dorsal to the foramen caecum and consisting of the *lingual tonsil*. The dorsal surface of the ventral part of the tongue is relatively smooth, and is dotted here and there by the *fungiform papillae*, of which there are in the neighborhood of two hundred. Fungiform papillae are especially abundant at the tip of the tongue, where they extend well over on the ventral surface. Along the sides of the tongue these papillae extend on the ventral surface to a slight extent. On that part of the dorsal surface of the tongue between the vallate papillae and the lingual tonsil the fungiform papillae are absent. The *vallate papillae* are two or three in number, on either side of the median line, and are arranged in the form of a V, whose apex is at the foramen caecum. The *filiform or conical papillae* are short and closely packed giving the tongue its relatively smooth surface. *Foliate papillae* are present along the sides of the tongue ventral to the lingual tonsil.

The mucous membrane of the ventral surface of the tongue just in back of the tip is elevated in the median line to form the *frenulum linguae*. Extending ventrally from the frenulum and on the under surface of the tongue is a rather deep sulcus which does not quite attain the tip. Beneath the tongue and on either side of the midline is a tuft of mucous membrane about one-fourth of an inch in length, on the upper border of which is the opening of the submaxillary duct.

Muscles of the tongue

The musculature of the tongue consists of an intrinsic and an extrinsic set of muscles. The intrinsic muscles are bundles which are disposed in longitudinal, transverse, and vertical directions. The *extrinsic muscles* are the styloglossus, hyoglossus, genioglossus, and glossopalatinus.

The *styloglossus muscle* (fig. 60) arises by a fleshy origin from the cranial two-thirds of the stylomandibular ligament. It inserts into the lateral aspect of the base of the tongue, where it overlies the insertion of the hyoglossus. At their origin the fibers of the styloglossus have a slightly caudal inclination, but as they pass to their insertion they tend to become horizontal. When the muscle contracts the tongue is retracted and slightly elevated. The muscle is supplied by the *hypoglossal nerve*.

The *hyoglossus muscle* (fig. 60) is flat and quadrilateral. It arises from the lateral aspect of the body of the greater cornu of the hyoid bone and inserts into the lateral surface of the base of the tongue. It is a depressor of the tongue and an elevator of the hyoid bone, and is supplied by the *hypoglossal nerve*.

The *genioglossus muscle* (fig. 60) arises by a tendinous origin from the dorsal surface of the symphysis of the mandible. As the fibers pass dorsally they radiate in a fan-like manner, the more caudal fibers attaining the dorsal extremity of the tongue. As the ventral and intermediate fibers pass into the tongue they are compressed laterally and have a linear insertion into the tongue substance immediately lateral to the midline. The ventral fibers can be followed to within a short distance of the tip. The caudal fibers serve to protrude the tongue; the ventral fibers to retract it after protrusion from the mouth. The muscle is supplied by the *hypoglossal nerve.*

The *glossopalatinus muscle* is described with the palate (v.s.).

THE PHARYNX

(Figs. 56, 59, 60)

The pharynx. This, comprising parts of the alimentary and the respiratory systems, lies ventral to the cervical part of the vertebral column, and extends from the base of the skull to the caudal border of the cricoid cartilage, where it continues into the esophagus. Ventrally, the pharynx consists of a series of apertures, by means of which it communicates with other cavities, and interposed solid structures. Laterally and dorsally the pharyngeal wall is musculo-membranous. The pharyngeal cavity is lined throughout with mucous membrane which is continuous with that of the cavities with which the pharynx communicates.

The pharynx consists of three topographic parts which are continuous with one another. The cephalic part lies dorsal to the nasal cavity and is referred to as the nasopharynx or postnasal space. The intermediate division is dorsal to the oral cavity and is named the oropharynx. The caudal part, which is dorsal to the larynx, is called the laryngopharynx.

The *nasopharynx*, which is exclusively respiratory in function, is limited dorsocranially by the ventral surface of the sphenoid and occipital bones; ventrocaudally, and partially separating it from the oropharynx and mouth, is the soft palate; ventrocranially are the internal nasal orifices, through which the nasopharynx communicates with the nasal cavity; and dorsocaudally is the communication with the oropharynx. The lateral wall contains the medial pterygoid plate, the superior constrictor muscle and musculature of the soft palate, namely, the levator and tensor veli palatini muscles. In the lateral wall, dorsal and somewhat caudal to the dorsal extremity of the inferior nasal concha, is the slit-like orifice of the *auditory tube* which establishes a communication between the cavity of the nasopharynx and that of the tympanum or middle ear.

The cavity of the nasopharynx is subdivided by a median partition or connective tissue septum which has been referred to as the membranous nasal septum. In the dorsal wall of the nasopharynx is the *pharyngeal tonsil*, which is continued into the membranous septum and which extends ventrally to its junction with the soft palate.

The *oropharynx* is both alimentary and respiratory in function. It extends from the dorsal border of the soft palate to the entrance into the larynx. Its dorsal and lateral walls, like those of the nasopharynx, are musculomembranous. The oropharynx communicates ventrally with the oral cavity through the faucial isthmus; cranially with the nasopharynx; and caudally with the laryngopharynx. In its lateral wall is the tonsillar fossa which lodges the *palatine tonsil*. The fossa is limited ventrally and dorsally by the glossopalatine and pharyngopalatine folds, respectively. The surface of the tonsillar fossa is smooth, and in it there is a relatively large slit-like opening which leads into a rather deep crypt. The tonsillar tissue is deeply placed in the pharyngeal wall just beyond and around the blind end of the crypt. The dorsal surface of the posterior part of the tongue is in relation with the oropharynx, and between it and the epiglottis are two depressions, the *valleculae*, one on either side of the glosso-epiglottic fold.

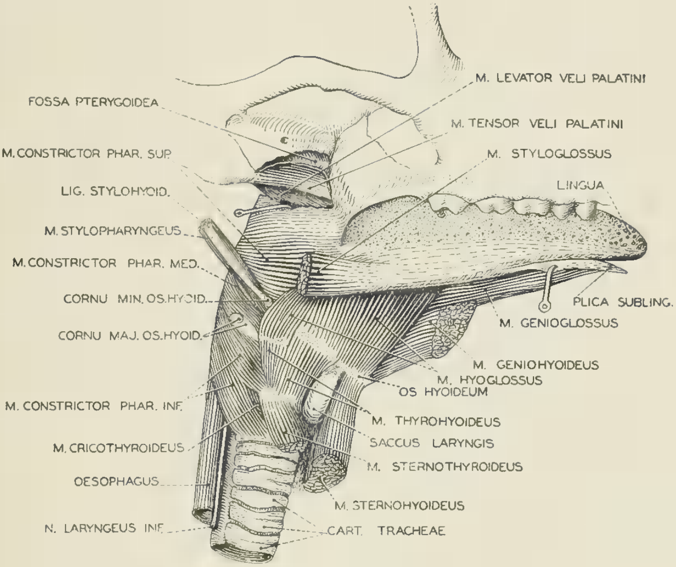

FIG. 60. Right lateral view of the muscles of the pharynx and associated structures.

The *laryngopharynx* lies dorsal to the larynx and is both alimentary and respiratory in function. Cranially, it is continuous with the oropharynx, and caudally it continues into the esophagus at the caudal border of the cricoid cartilage. Its lateral and dorsal walls are musculomembranous. Ventrally are the *aditus*, through which it communicates with the larynx, and the lamina of the cricoid cartilage. On either side of the midline the ventral wall presents a depression, the *pyriform fossa.*

Muscles of the pharynx

(Fig. 60)

The muscles of the pharynx are the superior, middle, and inferior constrictors, the stylopharyngeus, and the pharyngopalatinus which is common to it and the soft palate.

The *inferior constrictor muscle* consists of two parts which, at their origins, are separated by a considerable interval. The caudal part of the muscle arises from the external surface of the lateral part of the arch of the cricoid cartilage at its caudal border dorsal to the attachment of the cricothyroid muscle. The fibers at first pass dorsally and cranially at an angle of about 45°; the caudal fibers then assume a less oblique direction as they pass towards their insertion. At the insertion of the muscle the caudal fibers blend with those of the corresponding muscle of the opposite side and with the musculature of the esophagus. The cranial fibers attach to the caudal part of the pharyngeal raphe. The cranial portion of the inferior constrictor muscle arises from the external surface of the lamina of the thyroid cartilage under cover of the thyrohyoid muscle. The fibers pass dorsally, then cranially and insert into the raphe. Towards their insertion the more cephalic fibers of the cranial portion of this muscle overlap the caudal fibers of the middle constrictor.

The *middle constrictor muscle* arises from the external surface of the greater cornu of the hyoid bone. The cranial fibers overlap the caudal part of the superior constrictor muscle and insert into the raphe. The stylopharyngeus muscle, the stylohyoid ligament, and the glossopharyngeal nerve pass between the middle and the superior constrictors near their origins.

The *superior constrictor muscle* arises from the caudal part of the medial pterygoid plate, from the side of the tongue where it is more or less blended with the fibers of insertion of the styloglossus muscle, and from the oral mucosa between the medial pterygoid plate and the tongue. Its fibers pass dorsally and with a slight cranial curvature to their insertion in the raphe. Between the cranial border of the muscle and the base of the skull the wall of the pharynx is membranous and is heavily laden with glands. In this membranous interval are the auditory tube and the levator veli palatini and tensor veli palatini muscles.

The *stylopharyngeus muscle* arises in common with the styloglossus muscle and the stylohyoid ligament from the caudal surface of the petrous portion of the temporal bone. Its insertion is by means of a tendinous and connective tissue expansion through which it becomes attached to the greater and lesser cornua of the hyoid bone. A few muscle fibers attach to the caudal part of the stylohyoid ligament.

The *pharyngopalatinus muscle* has been described with the muscles of the soft palate (v. s.)

The pharyngeal muscles serve to constrict the lumen of the pharynx and, in deglutition, to propel the food toward the esophagus. The stylopharyngeus is also an elevator of the hyoid bone and the larynx.

The stylopharyngeus muscle is supplied by a branch of the *glossopharyngeal nerve*. The remaining muscles derive their supply from the *pharyngeal plexus*, which is formed grossly by fibers of the glossopharyngeal and vagus nerves together with branches from the superior cervical sympathetic ganglion.

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Chapter X

THE RESPIRATORY, DIGESTIVE AND URINARY SYSTEMS

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RESPIRATORY SYSTEM

Trachea. In its course down the mediastinum the trachea lies in front of and quite free of the esophagus. At its beginning it is, with the larynx, the most prominent structure in the neck, causing the esophagus to be flattened, and at its lower end it causes the whole arch of the aorta to occupy a left lateral position. The length of the trachea, from cricoid cartilage to its bifurcation, is 9.5–11 cms., and it is slightly flattened transversely with a diameter of 9 mm. Near its lower end, however, it becomes rounded, and slightly flattened anteroposteriorly near the bifurcation. It is composed of about twenty-seven cartilaginous plates which extend around the tube completely, but do not fuse where they meet posteriorly. Instead of fusing, the tips remain separated and the space between is filled in with muscle and other soft tissues. The plates are larger and more regular in the upper end; in the lower end they tend to be narrower and thicker. In the middle and lower regions are found a few incomplete plates, which do not encircle the tube but end shortly in blunt points; others may end by forking or by joining an adjacent plate (fig. 56). In these points the trachea of the rhesus monkey agrees with those of the so-called higher primates, but differs from those of certain of the Lemuroidea, in which the cartilages may be complete dorsally, thus forming uninterrupted rings. The soft tissues are folded in along the posterior line, making a narrow deep groove between the tips of the cartilages. At the lower end of the trachea may be found a typical "double arched" cartilage and on either side of this the two bronchi, right and left, are given off.

Bronchi. The right bronchus extends in an almost straight line from the trachea, but the left one comes off at a distinct angle. The eparterial bronchus leaves the right bronchus just after this tube comes from the trachea, but the left bronchus extends a considerable distance before subdividing, being thus much longer than its fellow on the right.

As the tubes are followed into the lungs they show less branching and less regularity than in man. The cartilages of the bronchi show the same general pattern as those in the trachea. Further in the lung tissue, however, the plates become true rings, completely encircling the tube.

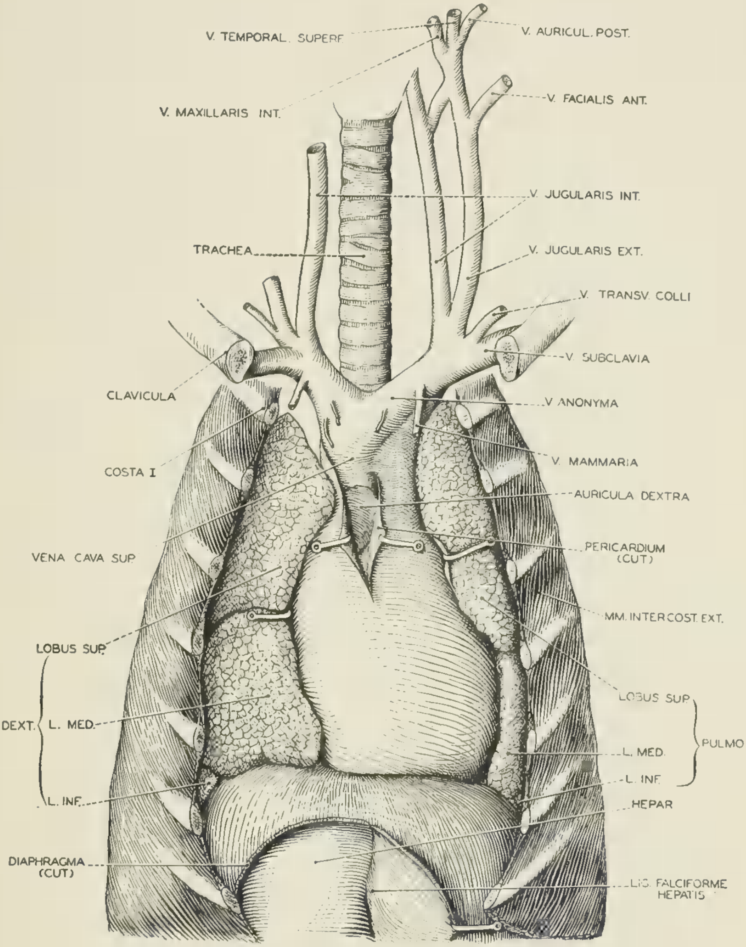

FIG. 61. The contents of the thorax, anterior view.

The whole tubular mechanism is lined by a thin mucous membrane, anchored to the cartilaginous wall by a narrow but firm submucosa. The surface is smooth and even, showing neither ridges nor folds to the unaided eye, and apparently few or no glands are present in the submucosa.

LUNGS. From a superficial anterior view the two lungs (pulmonales) appear quite similar; three lobes may be identified on each side (figs. 61, 62). Upon deeper inspection the middle lobe on the left side is smaller than the similar lobe on the right side. This is due to its giving place to the heart, thus producing the cardiac fossa, incisura cardiaca. Due to the great elongation of the thorax the dorsal portion of the inferior lobe extends in a tongue-like elongation markedly caudalward (fig. 62). In addition, the reflection of the pleura from the costal wall to the diaphragm produces a much deeper and narrower cleft than in man. The border of the lung in this vicinity is, as a result, much sharper and may be seen in places as a narrow flange of pleural membrane. It is further to be noted that the left interlobar clefts are not as deep as on the right side, and the lobes consequently are not as distinctly isolated. This point is variable, however, since in some specimens there may be found complete clefts producing entirely separate lobes. Fusion may, however, occur between the surfaces of two adjacent lobes, with obliteration of the interlobar cleft, the outline of the lobes being less clearly defined. The roots of the lungs exhibit the same general arrangement as in man. The eparterial bronchus occupies the uppermost dorsal position, on the right side, with the other bronchi just caudal to it (fig. 62). The pulmonary arteries lie just in front of and a little below the bronchi, and the veins lie still in front of and below the arteries. The arteries are well developed and branch more freely than the veins, and they appear to pass straight out into the lung mass. The veins, on the other hand, are less divided. For each lobe there is only one large vein, at least at the point of exit at the root, and it courses along the surface of the lobe for a considerable distance just beneath the pleura (fig. 62).

A striking deviation from the human lung pattern is found on the right side, in the instance of a buried accessory lobe (*lobus azygos*). This lobe is seen just caudal to the root of the lung, lying dorsally, and attached to the median surface of the inferior lobe (fig. 62). The attachment is by a narrow pedicle through which pass its nutrient and air structures as branches of those supplying the inferior lobe. The lobe proper may be expanded to good size (indeed in several instances it was nearly as large as the middle lobe), and it occupies a peculiar position. There is an oval opening lying just behind the vena cava and the right phrenic nerve, which admits into a closed space or recess directly behind the pericardium. This recess is lined by a pleural reflection from the right pleural cavity and is in reality a diverticulum of the latter, since it does not communicate with the left pleural space. In the natural state the accessory lobe passes through the opening by its pedicle, and the lobe proper occupies the recess.

The lungs of the rhesus macaque differ from those of man with respect to the presence of three lobes on the left side and an azygos lobe on the right side. In the orang-utan the lungs are normally non-lobate; the opposite extreme obtains in *Tarsius*, in which the number of lobes may exceed that found in the macaque.

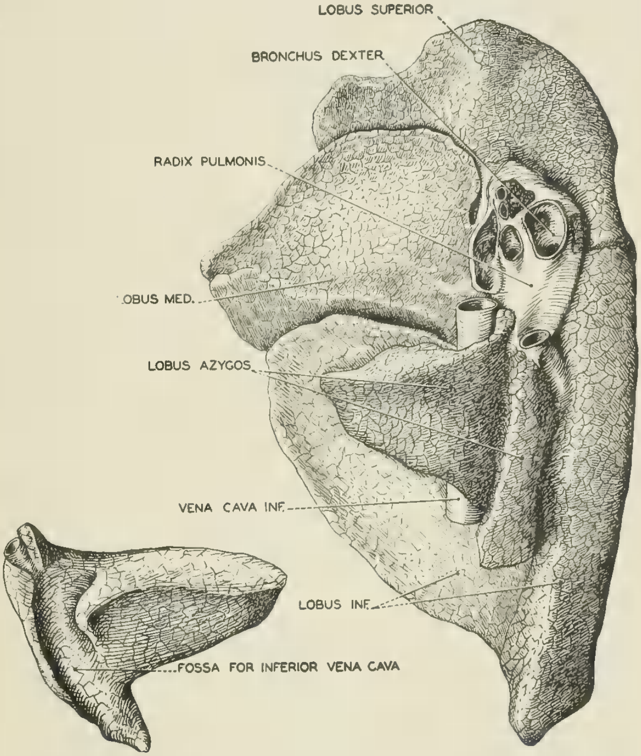

FIG. 62. Right lung, posterior surface. The insert shows the azygos lobe alone.

The blood supply of the trachea is from the arch of the aorta and its large trunks. Bronchial arteries leave the upper part of the thoracic aorta and follow the bronchi out into the lungs as nutrient vessels to these structures. The minute pattern of the lung is less distinct and less regular than that of man. The bronchioles, as well as their attending blood vessels, are fewer and larger than in man, but the meshwork of the air sacs is more extensive.

Pyramidal lobulations may appear on surface inspection (fig. 62), but in reality, on more minute study, no such sharp outlining is found within. The individual air sacs are much larger than in man, being easily seen with the unaided eye as a profusion of light spots on the pleural or the cut surface. The alveolar walls are, in turn, thinner and bear fewer capillaries than in man.

DIGESTIVE SYSTEM

Esophagus. The esophagus begins just dorsal to the arytenoid cartilage as a transversely flattened tube. It passes downward through the mediastinum directly behind the trachea and to the right of the aorta. At the lower end of the trachea it passes directly in front of the aorta and disappears through the crura of the diaphragm into the abdomen. Its length varies from 14 to 16 centimeters.

At its beginning and for 3 or 4 centimeters it is flattened, having a width of one centimeter; its two walls, front and back, are in contact. The lowermost fibers of the inferior pharyngeal constrictor muscle pass down into the tube for several centimeters and greatly increase its thickness. At about midway of its length it becomes more rounded with an increased diameter; the increase is in reality a dilation, since the wall here is markedly thinned. For several centimeters before reaching the stomach the tube becomes enlarged, due to the great increase in the circular muscle; it continues rounded for the remainder of its length.

There is a narrow but very elastic submucosal stratum interposed between the muscular layer and the mucosa. The mucosa is a thin but firm membrane, chiefly composed of a stratified squamous epithelium which shows some folding at the two ends of the tube but little or none in the midregion. Glands are grossly absent from all parts. Its blood supply is chiefly from the segmental branches of the aorta as this vessel passes downward through the mediastinum. In the upper region its supply comes primarily from the external carotid artery and its branches.

Peritoneum. In general the membranes and folds are simpler than in man, retaining a more primitive or embryonic status (cf. van Loghem). Indeed this more simple condition in the rhesus macaque lends itself most satisfactorily to a study of the mesentery in comparison with more advanced growth and greater complexity, as found in man. The entire digestive tube, with the exception of the first part of the duodenum and the first part of the colon, has a well defined free mesentery; that for the greater part of the colon is exceptionally broad (fig. 64). The line of attachment of the mesentery to the dorsal body wall is along the course of the abdominal aorta, primarily and prominently at the branching off of the coeliac and superior mesenteric arteries. A number of short folds and membranes are encountered in connection with the different viscera; these will be included in the description of the several organs.

Stomach. The stomach (ventriculus) is relatively larger than that of man, with the greatly enlarged fundus occupying a more extensive and lower region in the left abdomen. It is distinctly elongated and pear-shaped, with the pylorus, as the stem, passing to the right and curving backward to enter the duodenum (fig. 63). The axial line is a spiral rather than a curve, since the pyloroduodenal junction is much lower than the cardia. The lesser curvature is short and sharp, but farther removed from the liver than in man, hence the *gastrohepatic ligament* is broader. The ligament (fig. 63) is well developed and extends along the lesser curvature from the esophagus to just beyond the pyloroduodenal junction, where it ends in a sharp edge, bounding the foramen of Winslow anteriorly. Some fat and a few lymph nodes are found between its folds, and of its chief constituents the common bile duct lies nearest the edge,

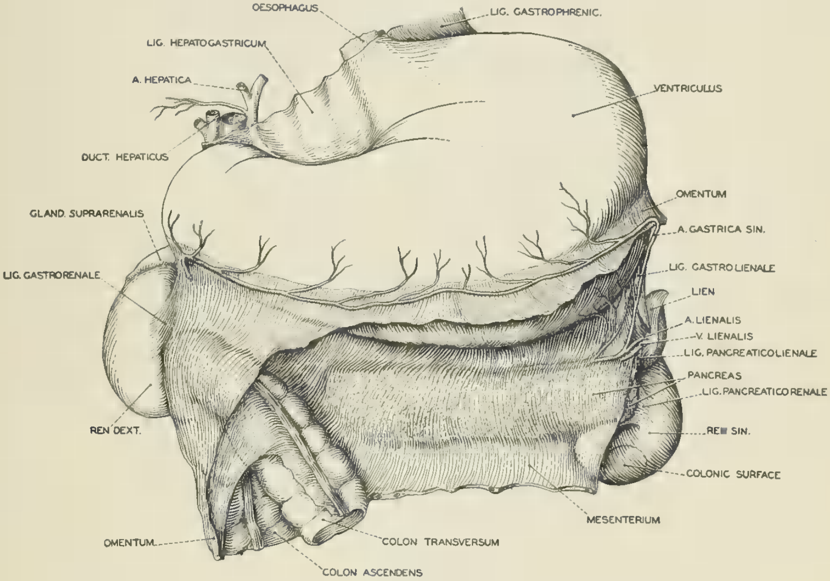

Fig. 63. Anterior view of the stomach and adjoining structures.

the portal vein comes next and a little behind, and the hepatic artery is to the left but a little in front of the vein (fig. 63). The right gastric artery leaves the coeliac axis and passes along the curvature between the sheets of the ligament, giving off branches to the stomach, and terminates near the pylorus in the hepatic artery. A small branch of this vessel supplies the gall bladder and occasionally a larger branch may pass downward behind the pylorus, into the region of the pancreas, as the pancreaticoduodenal artery.

When distended the greater curvature swings forward and places the stomach in a horizontal anteroposterior plane. The *greater omentum* is attached to the greater curvature (fig. 63) from the fundus to the pylorus and is an extremely large membrane, extending to all regions of the abdomen, even into the pelvis. It is, however, very thin and delicate and contains relatively few vessels and lymph nodes. A narrow fold of peritoneum on the left side, in line with the omentum, extends between the fundus and the adjacent left diaphragm as the *gastrophrenic ligament* (fig. 63). The left gastric artery runs between the two omental sheets following the greater curvature, but some 2 or 3 centimeters away from the gastric surface, and gives off numerous short branches to both surfaces of the stomach (fig. 63). Near the pylorus it can be followed downward to disappear behind the head of the pancreas and finally it joins either the right gastric artery or the coeliac axis, as the right division of the left gastric artery. In some cases the pancreaticoduodenal artery springs from this right division of the left gastric artery instead of the right gastric artery. Another reflection of the peritoneum in line with the omentum, the *gastrolienal ligament*, leaves the fundus at the extreme left and passes over to and anchors the spleen (fig. 63). Through this fold a few small arteries from the splenic artery pass over to the stomach in addition to those of the left gastric artery.

The capacity of the stomach, in moderate distension, is from 80 to 100 cubic centimeters. The walls are thin in the region of the fundus, but very thick in the pylorus. The muscles exhibit an arrangement similar to that of man, with probably greater irregularity in the fundic area. The pyloric canal is relatively quite long and is sharply marked off from the duodenum by a great thickening of the circular muscle, the *pyloric sphincter*. A well defined elastic submucosa is interposed between the muscle and the mucosa. The mucosa is quite thick and is responsible for the greater mass of the gastric wall. In the fundus it is smooth with only occasional low irregular ridges scattered here and there, but toward the pylorus the ridges become more numerous and are higher and more distorted. In the pyloric canal proper the ridges are more fixed than elsewhere and produce quite a labyrinthine surface. Scattered throughout the whole gastric surface the openings of the pits of the glands may be seen with the unaided eye. At the cardia there is a well defined line of junction between the mucosa of the esophagus and the stomach. According to the status of the wall the line may be smooth and even or it may be serrated and uneven, but always perceptible. At the pyloroduodenal junction a similar line of demarcation exists. Just beyond the sphincter fold the duodenum begins as a vestibular-like enlargement with a smooth, even lining; no ridges or folds appear here.

SMALL INTESTINE. The small intestine (intestinum tenue) consists of three parts, viz. duodenum, jejenum and ileum. The *duodenum* begins at the above-mentioned abrupt junction line as a simple enlargement, having a diameter of some 1.5–2.0 cms. It extends for some 4 or 5 centimeters closely attached to the dorsal body wall and has its diameter reduced to one centimeter or less. It then turns sharply headward for a few centimeters and enters the *jejenum* or the small intestine proper. There is thus a short loop in the course of the duodenum, but the left part is inconsequential. It passes imperceptibly into the small intestine proper, which shows surface features quite uniformly distributed throughout. The mesentery supporting the small intestine is gathered into a closely packed bunch of folds surrounding the superior mesenteric artery. The width of the membrane increases along the length of the intestine down into the *ileum* and to the caecum, where it may have a breadth of 10 to 15 centimeters from the body wall to the wall of the tube (fig. 64).

The wall of the small intestine is relatively thin; this is especially true of the muscular portion, where the circular layer is, however, thicker than the longitudinal. There is a narrow but well defined submucosa between the muscles and the mucosa, which, as in the stomach, makes up the greater part of the thickness of the wall. The mucosal lining of the intestine is fairly uniform throughout the entire length of the tube but shows several modifications characterising the two ends, the duodenum and ileum. No true plicae circulares are present anywhere, but folds may be seen throughout the tube and are of two types, the fixed and the transitory. The latter are functional products, appearing when the wall is contracted and disappearing in dilation. They are found in a transverse position on the wall, and in addition, in extreme contraction, folding in a longitudinal direction may occur. The fixed folds are confined to the proximal portion of the intestine and are best marked in the duodenum. They are disposed transversely on the sides of the tube, opposite to the line of the mesentery, and are not effaced by variations in the wall. The surface of the mucosa is noted to be of velvet-like appearance, produced by the villi, which can be seen with the unaided eye. They vary in structure in different parts of the intestine; those in the

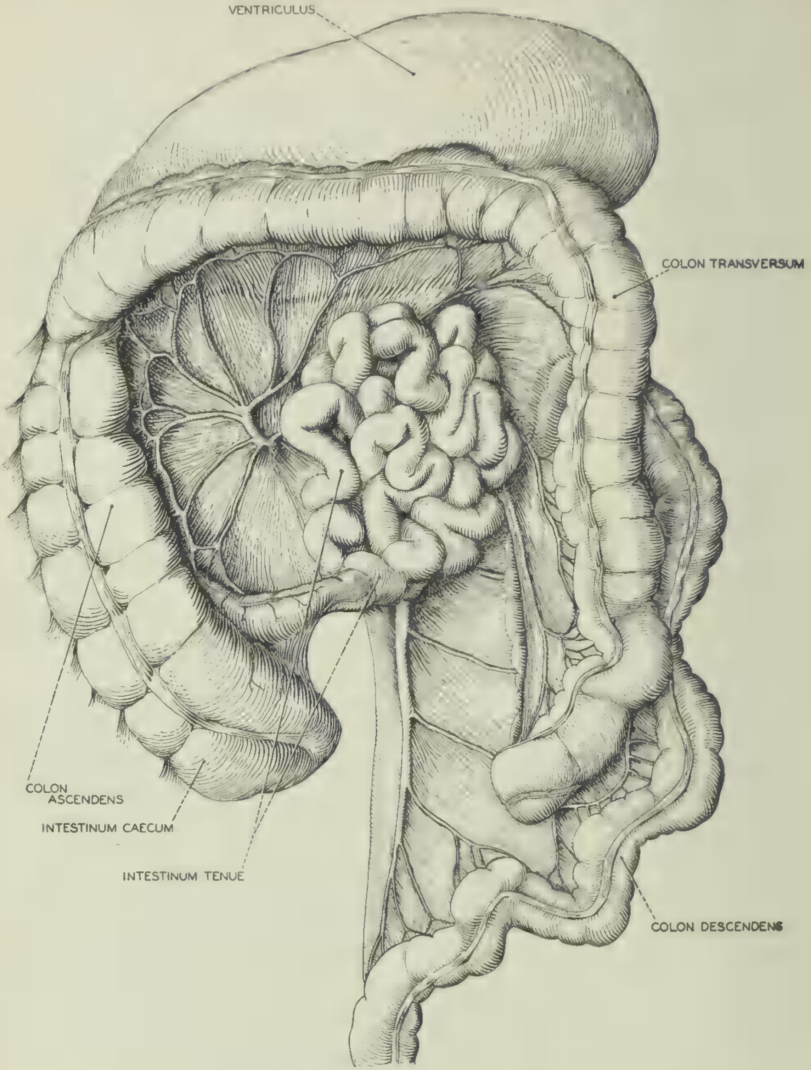

Fig. 64. The intestines, anterior view.

proximal portion, especially in the duodenum, have the form of small flanges, from 0.5–1.0 mm. long and 0.1–0.2 mm. thick, and are disposed in transverse axis to the tube. Those in the distal portion, the lower ileum, are true villi appearing as pile on a plush fabric, and in the mid-region there may be found a mixture of both types.

The blood supply of the small intestine is primarily from the superior mesenteric artery (fig. 82), the branches of which pass through the mesentery to the tube. As they approach the wall they break up into smaller branches which form loops or arches, and from these the terminal vessels pass, on both sides, around to a lateral position where they finally penetrate the intestinal wall. The right colic branch, from the superior mesenteric artery, supplies the first portion of the colon as in man (fig. 64).

Large intestine. On first inspection of the opened abdomen, the colon, instead of the small intestine, comes prominently to view (fig. 64). Usually a section of the bowel is seen extending from the upper right region obliquely downward into the lower left iliac fossa, covered only by the omentum. Upon deeper inspection this section is seen to be one part of a loop, the other part of which passes more deeply back to the upper left region. Beginning at the *caecum*, which lies a little to the right of the center of the abdomen, the *colon* passes upward into the vicinity of the right kidney. Here it makes a sharp turn downward to become this oblique portion. After making the turn of the loop, which may occur anywhere in the lower abdomen, even in the pelvis, the second portion passes upward into the region of the left kidney. Here it makes a second sharp turn and becomes the descending colon. There are thus blocked off the three parts of the colon, as in man, the ascending, the transverse and the descending. The chief differences in the rhesus monkey are the great length of the transverse part and a mesentery for the entire length of the bowel. This well defined mesentery does not, however, blur the identity of the three parts. The closer adherence of the first part to the body wall clearly identifies it, and the distribution of the inferior mesenteric artery exclusively to the descending part establishes its identity. The transverse part is little different from the similar loop in man, except that it is longer and has a broader mesentery.

The mesentery of the colon is continuous with that of the small intestine and varies in breadth and in content in its several parts (fig. 64). For the ascending colon it is more like a broad web-like meshwork than a true membrane. It contains no structures, vessels, nerves, lymph nodes, and serves mainly to attach the bowel to the body wall. The vessels to this part of the bowel approach it at the inner edge of the meshwork. The true mesenteric membrane anchoring the rest of the colon to the body wall contains all the typical structures, vessels, nerves, lymph nodes, as in the jejunal mesentery, and is attached to the medial taenia of the tube. It measures some 7–10 cms. in width and contains some fat, and rather numerous lymph vessels, in addition to its arteries and veins. The mesentery of the transverse colon has the greatest width, measuring some 12–15 cms., but contains few vessels and lymph nodes. The mesentery of the descending colon has a varying width of from 10 centimeters in the upper portion to barely a millimeter in the lower pelvis (fig. 64). It contains some lymph nodes and its blood vascular mechanism is distinctive; the inferior mesenteric artery courses through the base of the mesentery down to the rectum and gives off, in rather orderly fashion, nine or ten branches. These run to near the bowel, where they send off long sweeping arciform branches which anastomose with their neighbors to form primary loops. From these loops small terminal branches pass to the bowel, where the majority swing around, superficially, to the lateral taeniae before penetrating into the depth of the wall. This broad free mesentery, throughout most of the length of the bowel, permits great freedom of movement which results in the colon occupying the more prominent position in the abdomen. The small intestinal loops, consequently, are gathered into a rather compact cluster, in behind the loop of the transverse colon (fig. 64).

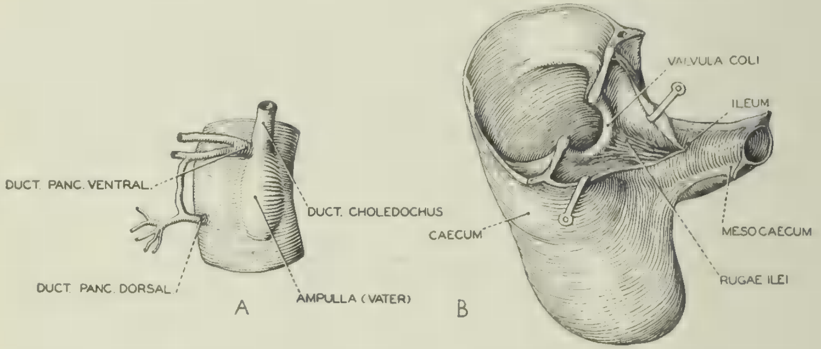

FIG. 65. A, section of duodenum, showing ampulla of Vater and entrance of the pancreatic ducts. B, the ileocecal junction.

The omentum is attached, by its posterior sheet, to the colon along the line of the anterior taenia of the transverse part (fig. 63). Its attachment to the ascending part is blurred by the meshwork adhesions of the peritoneum holding this part of the bowel to the body wall.

The colon has a normal length, from ileocaecal junction to anus, of 50–55 cm.; the first part being about 10 centimeters long, the transverse 30 centimeters and the descending 15 centimeters. The width varies from a few millimeters in the descending portion, where there is marked contraction, to several centimeters, chiefly in the caecum and ascending part, where marked dilation may be noted. There is no appendix, but the caecum is drawn out out into a rather distinct cone, with a prominent apex, where the three taeniae fuse into a complete sheet covering it (fig. 64). A vermiform appendix is found among primates only in man, the four anthropoid apes, and in the lemur *Nycticebus*. There is a well formed membrane, the mesocaecum, joining the cone to the ileum, which extends for some 3 or 4 centimeters along the small intestine.

The structure of the colon is very similar to that of man. Three distinct, well formed *taeniae* extend throughout the whole length of the bowel, with typical rows of sacculations between them (fig. 64). One is impressed by this pattern, so well formed and typically adjusted, with the suggestion that the taenial bands act as strong fixed longitudinal cables against which the circular muscle fibers pull, in tripartite colonic peristalsis, thus producing clefts and sacculations. The *ileocaecal junction* is distinctive; the lining of the ileum, submucosa and mucosa protrudes into the caecum for 0.5–1.0 cm. in the form of a flattened cup (fig. 65 B). On either side of the cup, anterior and posterior, a ridge extends horizontally along the wall of the caecum. The rim is flattened vertically, parallel to the long axis of the bowel, with a diameter of 1.5 centimeters. At the bottom of the cup the mucosa is thrown into a number of folds, but near the rim the surface remains smooth. The mucosa of the colon presents ridges and folds of two general types: (1) Ridges which are the products of muscular contraction; these vary in size and shape, are numerous in the descending portion, where there is greatest contraction, and absent from the large saccules. (2) There are small irregular elevations distributed throughout the whole lining of the bowel, in the form of a mosaic of nodules; they are not affected by even marked dilation excepting the largest saccules, where they become a little broader and flatter.

The colon ends in a well developed *rectum*, where the pattern changes sufficiently to merit special attention. It measures some 6–7 cms. in length and 3–4 cms. in width and flattened anteroposteriorly (fig. 66). At the upper end there are two well marked folds, one on either side, the first to the left and the other a little lower down on the right. The three taeniae spread out and blend into a uniform layer of muscle just below the first fold. Both muscles, circular and longitudinal, are greatly thickened toward the lower end of the rectum, but sacculations as well as taeniae are absent. The anus is a short transversely flattened canal opening to the exterior, measuring 1.5–2.0 cms. in long diameter, with the anterior and posterior lips close together in the living state. A well defined internal sphincter ani muscle is lodged at the inner border of the anus; it is an enlargement of the circular muscle at this point. An external sphincter ani muscle surrounds the whole width of the anal canal

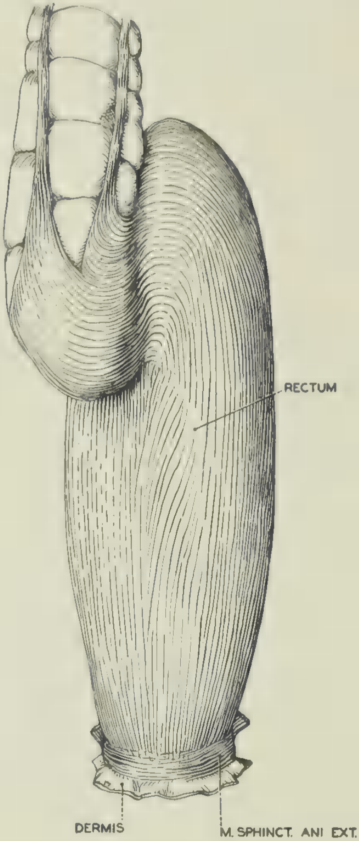

FIG. 66. The rectum.

and into it the longitudinal muscle of the rectum is inserted. It likewise receives the insertion of a pair of muscles, one on either side, which take origin from the anterior surface, laterally, of the vertebral column (fig. 39, 66). These in contracting doubtless aid in effecting a transverse flattening of the anal canal.

The interior of the rectum is marked only by a few low transverse ridges. The hand lens, however, reveals the mouths of the crypts, being here larger and more numerous than higher in the bowel.

Liver (figs. 61, 67). The liver (hepar) is distinctly of a primitive type, having a right and a left lateral lobe placed dorsally, and a single large ventrally placed central lobe (fig. 67) (cf. Ruge, 1906). It fills the greater part of the subphrenic space in the abdominal cavity and causes the stomach to occupy a lower and more horizontal plane than in man. The ligaments are similar to those of man; the *ligamentum teres* is, however, lodged more deeply in the interlobar fissure of the central lobe. The *falciform ligament* is a narrow membrane having a long line of attachment, up over the prominent dome of the central lobe back to the region of the hepatic veins. The *coronary ligament* is a narrow double sheet with its two triangular extensions curving around the esophageal sulcus, helping to anchor the lateral as well as the central lobe to the diaphragm. The lobes of the liver are, however, more irregular than in man. The *right lateral lobe* is more intimately attached to the *central lobe*, with only a shallow cleft between; the *left lateral lobe* is quite free from the central lobe, having only a fibrous attachment to it. This left lobe may have a separate ligament aiding in attaching it to the left diaphragm. The *quadrate lobe* is much narrower than in man and the *caudate lobe* is distinctive in that it almost encircles the inferior vena cava. The *portal fissure* is short and lies just in front of the vena cava, with the arrangement of entering structures, hepatic duct, portal vein and hepatic artery, as in man. As the vena cava passes by the liver it receives venous tributaries from the right lateral lobe and the right side of the central lobe only, but just before it penetrates the diaphragm to enter the heart it receives several large veins from the left portion of the central lobe and an extra vessel from the left lateral lobe. This left hepatic vein may also drain an area from the left diaphragm, receiving the flow through a small vein which joins the hepatic vein some distance away from the vena cava. The caudate lobe almost completely encircles the vena cava. This lobe may show several anomalous appendages in the lower region.

The gall bladder (*vesica fellea*) is a greatly elongated thin-walled sac which lies on the caudal surface of the central lobe; it scarcely extends beyond the free border of the liver (fig. 67). Its cystic duct joins the hepatic duct not far from the portal fissure and is accompanied backward by a small cystic artery. The lining of the gall bladder shows a

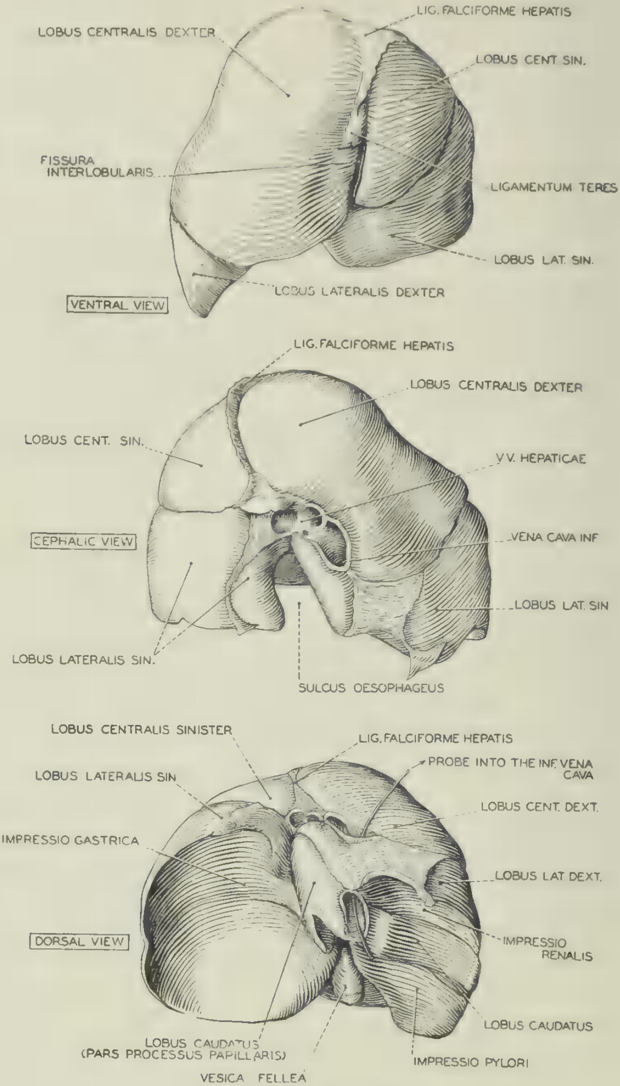

Fig. 67. The liver.

mottling of small ridges and nodules which extend into the duct and here become organized into a distinct pattern of spiral and circular folds. These folds are quite firm and effectively retard the flow of the bile through the duct. *Glisson's capsule* is a thin and delicate membrane which easily strips from the liver substance. It covers the gall bladder entirely, preventing it from becoming pendulous anywhere through its length, and follows the vessels into the interior of the liver. Here it assists in isolating the lobules, which are larger and more distinct than in man. The portal vessels, likewise, are larger but show less branching than in man.

Pancreas. The pancreas lies just behind the stomach in transverse axis (fig. 63). The head, much smaller in proportion to the body than in man, lies closely applied to the left surface of the first portion of the duodenum and is covered by the pyloric end of the stomach. The tail extends toward the spleen, but is separated from it by a distance of several centimeters, and is supported in a fold of peritoneum which is reflected from this body, the *pancreaticolienal ligament* (fig. 63). The gland is from 8–10 cms. long and from 1.5–2.0 cms. broad; the head, little more than a bend in the body, measures 2–3 cms. in length and the same in breadth. On cross section the body is triangular in shape with the broadest surface facing forward, and a narrow posterior cephalic and a caudal surface each facing backward. To the cephalic border of the broad anterior surface is attached a membrane which extends from the posterior surface of the stomach near the cardia and the adjacent body wall. It covers the anterior surface of the pancreas and then extends beyond it as the anterior sheet of the mesocolon. The splenic artery and vein course along the cephalic border of the anterior surface to reach the spleen. There is a loose feltwork of reticular fibers surrounding and extending into the interior of the gland, in the meshes of which are lodged the small irregular lobules. The *ducts* of the gland are, as in man, two in number. One duct joins the common bile duct in the *ampulla duodeni* (Vater) and opens either separately into the duodenum or in close connection with the common duct (fig. 65A). The other enters separately into the duodenum quite removed from the ampulla; its aperture is to the left and 1.0–1.5 cms. away. In the head of the pancreas there is a distinct duct which unites the two main ducts (fig. 65 A).

The blood supply to the pancreas is through the pancreaticoduodenal artery and some small recurrent branches from the splenic artery, and occasionally a few from vessels which pass over to the pancreas from the right gastric artery.

Spleen. The spleen (lien) lies in the upper left portion of the abdomen, just below the diaphragm, adjacent to the left aspect of the fundus of the stomach (fig. 63). It is invested by peritoneum, by which it is attached to the stomach (*gastrolienal ligament*), to the pancreas (*pancreaticolienal ligament*), and to the left kidney (*phrenicolienal ligament*). Its structure is similar to that of man, except that it is more triangular in cross-section and is relatively more elongated.

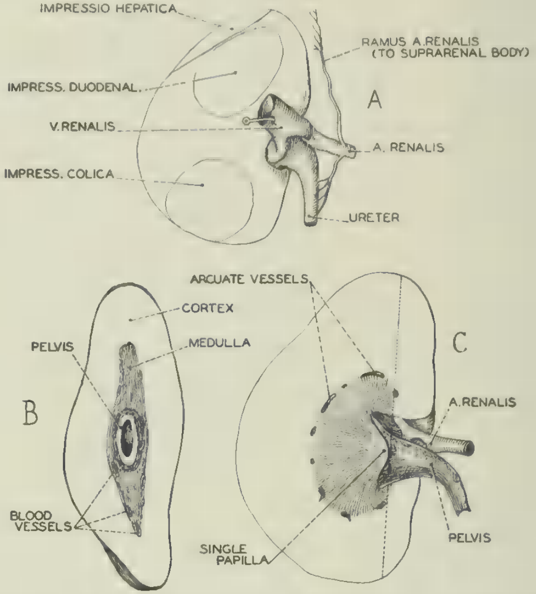

Fig. 68. The kidney. A, anterior surface of right kidney. B, sagittal section of right kidney. C, frontal section of right kidney. The dotted line shows the position of B.

URINARY SYSTEM

Kidney. The kidneys of the rhesus monkey differ strikingly from those of man. The left kidney is much lower in the abdomen than the right one (fig. 84). The condition is apparently due to the structure of the liver, which has a left lateral lobe that requires more room in this region. As a result of this the fundus of the stomach, as well as the left kidney, is forced to a lower level on this side. Except for the difference in size and position the two glands are similar, and may be included in one description. The kidney is firmly anchored to the dorsal body wall by a fibrous network, which attaches to about four-fifths of its posterior surface; the peritoneum covers the remainder, including the anterior surface. It is unusually flattened and is irregular in outline, the cephalic pole being smaller and sharper than the caudal pole. The right kidney measures about 3.5 cms. in length, 2.5 cms. in width, and 1.5 cms. in thickness, or less, and the left one is slightly larger in all dimensions. There is little or no perirenal fat, and the capsule is distinctive, more strikingly in the inner layer. There is a thin outer layer, a feltwork, which covers the body and extends out upon the entering structures at the hilus. It likewise extends up over the suprarenal gland and is the chief structure anchoring that body to the kidney. This outer layer can be easily removed from the underlying second layer by tearing the intermediate light feltwork attachments. This deeper layer is thin, but is more distinctly a membrane. It is quite firm and is closely applied to the surface of the kidney, dipping in at the hilus, but it does not extend up over the suprarenal body. It is applied to the surface much like a closely fitting rubber glove. There are no fibrous adhesions to the kidney substance, however, and once a cut is made it comes away as freely and smoothly as a glove.

The hilus is unusually small for the size of the gland, and the structures passing through it are also small. The rim is smooth and sharp, and no fat is found within its depth. The renal vein is the largest of the entering structures and is ventral to the artery. Just within the hilus it is formed by an anterior and posterior tributary, draining the two respective regions, and from between these two the ureter is seen emerging (fig. 84). The renal artery passes behind the vein in its course from the aorta, but just before entering the hilus it passes above the vein and divides into its two primary divisions, the anterior and posterior branches. The artery is most cranial, the ureter most caudal, and the vein is between the two. The anterior division of the artery usually subdivides into two branches and the posterior into three, serving the respective areas. Just before dividing the renal artery gives off a small branch which runs to and supplies the suprarenal body; another is sent to the ureter (fig. 82) (cf. chapter XIII).

The interior of the kidney is distinctive in respect to several points of structure. The *pelvis* is small and opens into one vertically flattened calyx. Entering the calyx there is a single *papilla*, or ridge, of kidney substance which is the apex of the whole renal mass (fig. 68). This condition is normal in other primates. The subdivisions of the artery pass exclusively to the two regions of the kidney, front and back, and on either side form distinct arches. From these arches terminal branches are distributed to both the cortex and medulla. The veins, in like manner, are formed into arches and ultimately converge into the two emerging veins at the hilus, which fuse, just above and in front of the pelvis, into the renal vein. There is no communication between the two main divisions of the arterial system, but there may be found, at several places, free union between the veins.

There is a distinct division of the kidney mass into a *cortex* and a *medulla*, which can be detected by the unaided eye (fig. 68). The arciform arteries and veins occupy the boundary zone between the two areas and, likewise, can be easily detected. Due to the thinness of the kidney the medullary portion is massed in the cephalic and caudal regions, and greatly reduced at the sides.

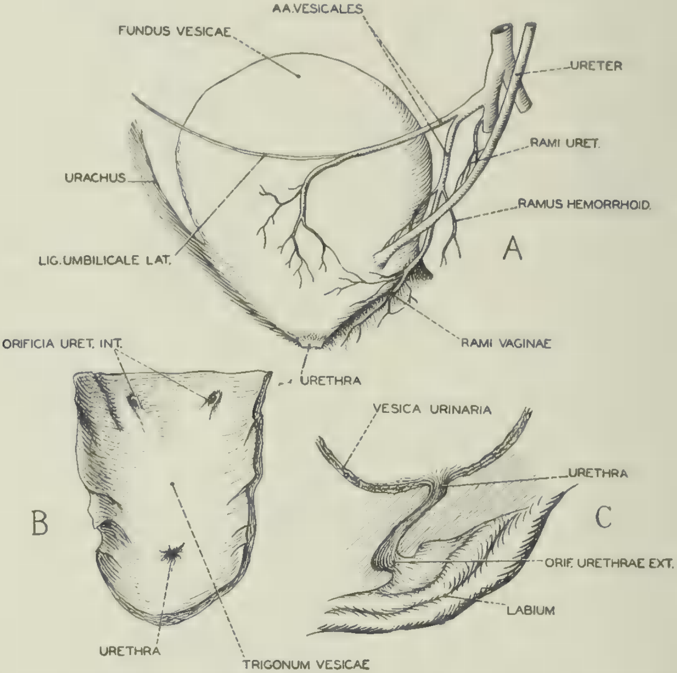

FIG. 69. The bladder and the female urethra. A, left side view of bladder, distended showing the arterial supply. B, inner surface of the bladder, looking down upon the urinary trigone. C, sagittal section, showing course of the urethra.

As the renal veins leave the kidney they are entered by the suprarenal veins, on the left side directly into the upper border, but on the right side usually quite on the posterior surface (fig. 84). On the left side the left ovarian vein can be seen entering the renal vein on the caudal border; the right ovarian vein enters the ascending vena cava lower down.

Ureter. The ureters pass downward behind the peritoneum, and over the common iliac vessels, into the pelvis. In their lower course they are closely accompanied by the spermatic (ovarian) vein and artery (figs. 39, 71, 75, 76). The left ureter measures some 12–15 cms. in length; the right one is 2 or 3 centimeters longer. The diameter is 1.5–2.0 mm.; it is slightly larger at the pelvis. It is composed of a firm muscular wall, and is lined by a transitional epithelium thrown into eight to twelve longitudinal folds, easily seen with the naked eye. Its blood supply is from the renal artery and the anterior division of the hypogastric artery direct and also from the inferior vesicular artery.

Bladder. The bladder (figs. 69, 76) is relatively large, having a capacity of from 60 to 80 cc. It occupies a rather extensive space in the pelvis, even when empty, crowding the uterus and rectum (fig. 76). It is rather firmly anchored to the anterior abdominal wall by a small strand of urachus fibers and the two obliterated umbilical arteries. It rests upon the anterior surface of the vagina by its *trigone*. This part of its wall is much thicker than any other portion and is quite free of folds and ridges (fig. 76). At the sides of the trigone and elsewhere numerous folds and ridges occur, especially when the vessel is empty. The two ureters enter the bladder about 2 centimeters apart and form the base of the trigone (fig. 69). The lower opening of the ureter is guarded by a thin, sharp-edged fold, so curved as to direct the urine forward and to the *urethral opening*. This exit lies a considerable distance in front of the ureters, 3 or 4 centimeters, and is much larger (fig. 69). Its rim is slightly elevated and is thrown into seven or eight folds which are the beginning of as many ridges running through the urethra proper.

Urethra. The urethra presents several peculiarities in the female (figs. 69, 76). It follows a broad S-shaped course from bladder to vulva, and measures about a centimeter in length It gradually expands in diameter and just before opening into the vulva is dilated into a small vestibule. The opening proper is distinctive in that it is lodged in a rather large tubercle just between the two labia minora. The tubercle is more correctly a pair of folds, one on either side, which guard the urinary meatus (fig. 77).

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Chapter XI

THE REPRODUCTIVE SYSTEMS

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THE MALE GENITALIA

Scrotum (fig. 70A). The testes of the rhesus macaque are located outside the body cavity in a loose bag of skin, the scrotum. In adults the scrotum may become semipendulous. Contrary to the opinion of several observers, most catarrhine monkeys, including the macaque, possess a well-developed scrotum. The scrotal skin is puckered or wrinkled and a trace darker in color than the surrounding skin. It is relatively sparsely covered by hair which differs slightly in color from the body hair. In the adult there is scarcely any trace of a median scrotal raphe (raphe scroti). The perineum is excessively long in the male, in contrast to the female in which it is exceedingly short. Hence both scrotum and penis lie relatively far anteriorly over the symphysis between the groins. The scrotum is postpenial, although the short penis is actually located within its anterior border (fig. 70A). The scrotum is separated from the anus by a long perineum to either side of which, over the ischia, lie the ischial callosities (callositates ischiorum).

The scrotum possesses a well-developed tunica dartos, a layer consisting of smooth muscle fibers and connective tissue which is connected with the fascia of the penis and the superficial fascia of the abdomen, thigh and perineum. It is continued in the median plane as a well-defined septum scroti which separates the two halves of the interior of the scrotum. Beneath the tunica dartos is a layer of loose areolar connective tissue.

Cremasteric fascia. Internal to these are the cremasteric fascia (fascia cremasterica) and the cremaster muscle (m. cremaster). The cremasteric fascia is a continuation downwards of the superficial abdominal fascia, as well as of the aponeurosis of the external oblique abdominal muscle. It also receives fibers from the membranous tissue, characteristic of the macaque, which lies between the external and internal oblique muscles (Mijsberg).

Cremaster muscle (figs. 70A, 70B). This is exceedingly well-developed in the full-grown, healthy macaque. It is easy to demonstrate by dissection that the cremaster has three bundles of origin: (1) from the m. obliquus internus; (2) from the m. transversus abdominis; and (3) from the upper border of the pubic bone (fig. 70B). The lateral portion of the muscle takes origin from the first two sources; the medial portion, from the pubic bone. The muscle appears to be derived about equally from these three sources. The lateral bundles of origin do not unite with the medial bundle until they reach the scrotum, where the fibers join and interlace. A small bundle of fibers of the m. transversus abdominis, instead of joining the cremaster, spreads out fan-like on to the spermatic cord between the two origins of the cremaster muscle (fig. 70B).

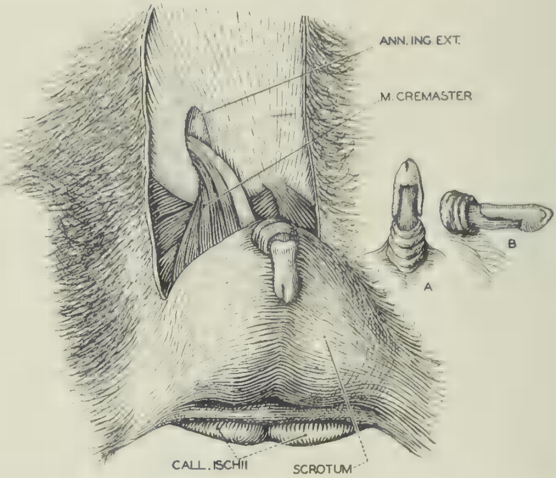

Fig. 70A. External genitalia of an adult male, with a dissection of the anterior abdominal wall. A, the penis seen from below. B, the penis seen from the side.

There is, internal to the cremaster muscle, an ill-defined tunica vaginalis communis, which is a continuation of the fascia transversalis of the abdomen, and internal to this the parietal layer of the tunica vaginalis propria.

Spermatic cord and testis. The spermatic cord extends from the abdominal inguinal ring (annulus inguinalis abdominalis) to the posterior margin of the testicle and contains the ductus deferens, as well as the spermatic arteries, veins, lymphatics and nerves. The testis is an ellipsoidal structure with the epididymis extending along its posterior border. In the adult the testes lie fully within the scrotum.

The relationships of the tunica vaginalis propria to the testis and spermatic cord are interesting. The cavum vaginale testis communicates, as in most monkeys, with the peritoneal cavity by an open processus vaginalis. At the annulus inguinalis abdominalis there is in front of the ductus deferens a narrow patent slit forming a communication between the processus vaginalis and the peritoneal cavity. Below this point the processus vaginalis widens out gradually toward the cavum vaginale testis. The spermatic vessels and the ductus deferens follow their courses in a membranous duplicature of the wall of the tunica vaginalis propria, so that there is formed a thin, broad mesentery which at its free border encloses the spermatic vessels. The ductus deferens lies in this mesentery on its mesial aspect about midway between the root of the mesentery and its free border.

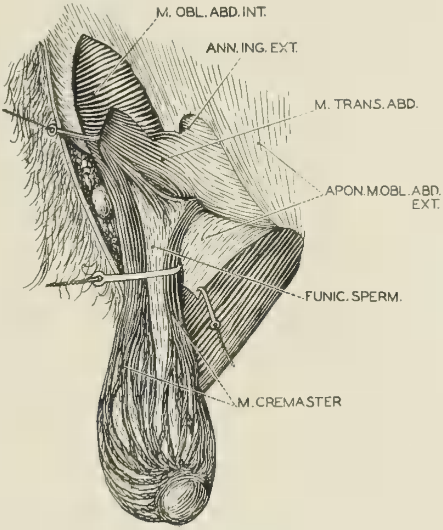

FIG. 70B. Dissection of the right inguinal region of an adult male, showing the cremaster muscle.

The testes and epididymis lie relatively free; the entire testis and fully four-fifths of the epididymis are enclosed by the visceral layer of the tunica vaginalis. The head and a large fraction of the body of the epididymis are attached to the parietal wall of the tunica vaginalis by a thin mesentery, the mesepididymis, which is a direct continuation downwards of the aforementioned mesentery of the tunica vaginalis funiculi spermatici. In this mesepididymis are located the spermatic vessels and the ductus deferens. Only the lower fifth of the epididymis (cauda epididymis) is firmly fixed and devoid of a serous investment. In consequence of this relatively slight fixation of the testis and epididymis, these organs are much more mobile than in man.

Descent of the testes. Statements to the contrary, the testes of the adult rhesus macaque lie completely within a well-developed scrotum. From observations on healthy, developing animals of the Carnegie Colony, it has been ascertained that descensus into the scrotum takes place some time in the fourth to fifth years after birth. For a relatively long period at puberty, however, the testes may return periodically into the inguinal canal. Prior to their descensus, the scrotum is represented by a narrow transverse fold of loose skin extending from groin to groin just behind the penis.

Recently the observation has been made (Wislocki) that during late fetal life and at birth, the scrotum of the rhesus monkey is swollen and as a rule contains descended testes. Shortly after birth the testes ascend into the inguinal canals and the scrotum retrogresses to become the above-mentioned transverse fold of skin characteristic of the juvenile period. As explained above, descensus occurs again at puberty. Similar, although not identical changes (swelling, degenerative changes in testes) around the time of birth, have been described in the human reproductive tract. These have been ascribed to hormonal factors. Engle (1932) has induced descent of the testes experimentally in juvenile macaques by administration of the gonadokinetic hormone from pregnancy urine or anterior lobe of the hypophysis. In contrast to the macaque and in resemblance to man, the testes in the chimpanzee descend permanently as a rule in the late fetal life.

THE DUCTUS DEFERENS. Upon leaving the inguinal canal, the ductus deferens bends sharply and follows a course towards the prostatic urethra (fig. 71). As it does so, it crosses the ureter. There is no distinct ampulla ductus deferentis in the region of union of the ductus deferens with the duct of the seminal vesicle; there is at most at this place a slight thickening of the wall of the duct.

THE SEMINAL VESICLES. The seminal vesicles (vesiculae seminales) are two lobulated masses exceeding, relatively, in the healthy, mature rhesus macaque, by far their size in man (figs. 71, 72). They communicate, one on either side, with the lower end of the ductus deferens. The lobules of the organ are bound together by connective tissue, which on the surface constitutes a capsule. The coiled, tubular mass, upon dissection, can be partially unravelled into a series of secondary and tertiary tubes or diverticula which communicate with a primary tube at the base of the organ. There are upwards of fifteen secondary branches and a lesser number of tertiary ones. Nothing short of corrosion preparations or reconstructions will give an exact answer to the topography of this structure. In its branching it is distinctly more complex than the human, which is described as a coiled tube with simple diverticula.

The prostate and prostatic urethra. The prostate (prostata) in the adult animal is a compact organ of conspicuous size situated on the posterior aspect of the prostatic urethra (pars prostatica urethrae; figs. 71, 72). In conformity with other monkeys and differing from the human, the prostate does not form a ring around the urethra, but lies solely on the posterior surface of the urogenital canal (figs. 71, 72). Hence the anterior lobe of human anatomy is totally lacking.

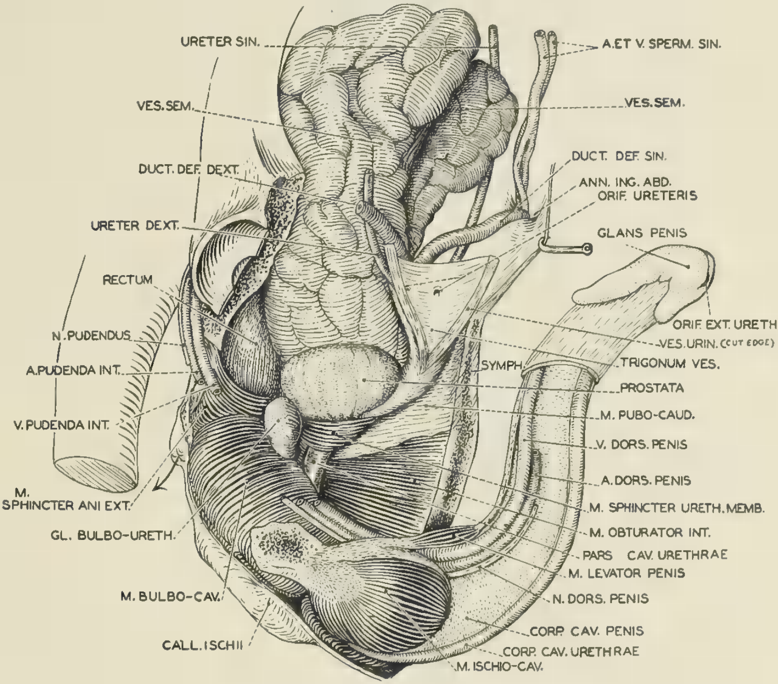

Fig. 71. Dissection of the penis and the accessory genital glands of an adult male.

Mijsberg recognizes in the prostates of monkeys, including the macaque, distinct caudal and cranial lobes besides smaller, less distinct, lateral lobes. He homologizes the cranial lobe with the isthmus prostatae or lobus medius of man. This lobe in monkeys is more extensive than in man and surrounds the ductus ejaculatorii as they perforate the prostate obliquely to reach the urogenital sinus.

In the posterior wall of the prostatic urethra the orifices of the ductus ejaculatorii and the openings of the prostatic ducts are located (fig. 72). On the summit of a prominent seminal crest (colliculus seminalis) a minute transverse slit (utriculus prostaticus) can be seen. To either side on the margin of the colliculus the ductus ejaculatorii enter the urethra. The openings of the prostatic ducts are visible only under slight magnification as a series of six to eight pores located bilaterally upon the lateral surface and margin of the colliculus. Above the colliculus no well-defined crista urethralis is present, but below it there is a definite ridge. At the lower margin of the colliculus at the base of the crista urethralis there are a number of minute papillae.

The membranous urethra. The membranous urethra (pars membranacea urethrae) perforates the urogenital trigone (trigonum urogenitale) and is surrounded by a layer of muscle (m. sphincter urethrae membranaceae). On either side of the membranous urethra is an oval Cowper's gland (glandula bulbo-urethralis) (fig. 71), the thin duct of which opens into the beginning of the cavernous portion of the urethra.

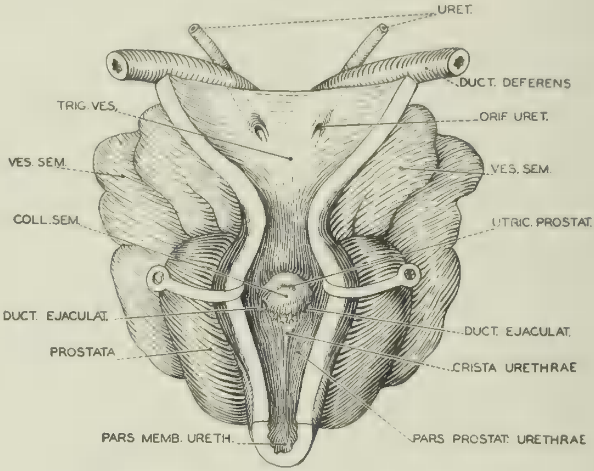

Fig. 72. Prostate, seminal vesicles and prostatic urethra of an adult male.

The cavernous urethra. The pars cavernosa urethrae runs within the corpus cavernosum urethrae and the glans penis.

The penis. The most conspicuous constituents of the penis are the erectile corpora cavernosa penis. They arise from the medial borders of the inferior rami of the ischia by stout, connective tissue fibers. The two crura converge beneath the symphysis pubis so that their sheaths (tunica albuginea) fuse to form a median septum. The corpora cavernosa extend anteriorly into the excavated part of the glans penis. The corpora cavernosa have a relatively thick tunica albuginea, and throughout much of their length the median septum disappears, so that the cavernous tissue within them becomes an unpaired body (fig. 73, A and B). Dorsal to them in the fascia penis run the arteriae dorsales penis and the vena dorsalis penis.

Beneath the corpora cavernosa penis lies the corpus cavernosum urethrae. In the rhesus monkey the ventral groove in the corpora cavernosa penis to receive the latter is relatively shallow. The corpus cavernosum urethrae is a cylindrical mass of cavernous tissue surrounding the urethra (fig. 71). It passes anteriorly into the glans penis while it arises as a swelling (bulbus urethrae) lying principally between the urethra and the bulbocavernous muscle and attached to the urogenital trigone. Due to this relationship, the urethra, for a short distance, upon emerging from the urogenital trigone (m. sphincter urethrae membranaceae) is not completely ensheathed. The bulbus urethrae possesses along its dorsal surface a median ridge which continues into a stout median septum separating the bulbocavernous muscles.

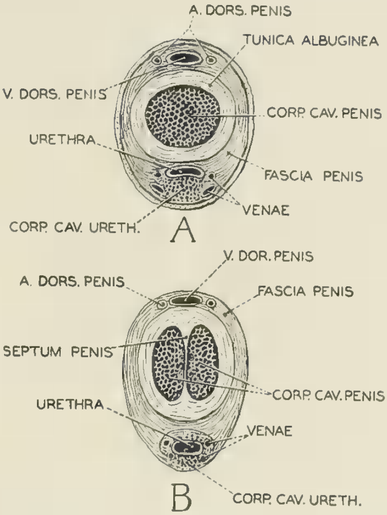

Fig. 73. Cross-sections of the penis. A, one centimeter behind the glans. B, three centimeters behind the glans.

The musculature of the penis (also see Chapter VII). The *m. ischiocavernosus*, which is a shorter, more stout-bellied muscle than in man, arises together with the crus of the corpus cavernosum penis from the lower ramus of the ischium (figs. 47, 48, 71). In section through the penis it is found as a fleshy mass forming a hemicircle around the corpus cavernosum. It inserts into the tunic of the latter and into the fascia of the penis.

The *m. bulbocavernosus* is an extremely stout muscle which lies posterior to the ischiocavernosus muscle (fig. 71). It arises from a strong median septum, an extension of the tendinous raphe attached to the border of the bulbus urethrae. Its fibers end principally in the fascia encircling the bulbus urethrae; few if any fibers go to the angle of junction of the crura penis. The posterior part of its raphe of origin receives fibers from the well-developed m. sphincter ani externus, so that the two are intimately joined.

The *m. levator penis* is a small muscle, characteristic of monkeys, including the macaque, and present only as a rare variation in man, which arises from the ischium just medial to the m. ischiocavernosus (figs. 48, 71). The tendons of the delicate muscles from the two sides unite into a common tendon which runs along the dorsum of the penis to insert behind the glans into the fascia of the penis. The dorsal artery, vein, and nerve of the penis pass beneath the body of the muscle between it and the m. ischiocavernosus to reach the dorsum of the penis (fig. 71). The action of this muscle is to elevate and straighten the pendulous end of the penis.

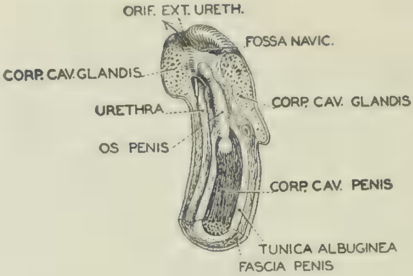

FIG. 74. Median section through the distal end of the penis.

THE GLANS PENIS. The glans penis has the shape of a cap which extends quite far back on the dorsum of the penis (figs. 70A, 71, 74) The pars cavernosa of the urethra pierces the glans to open as the external urethral orifice. Within the glans the lumen of the urethra is dilated (fossa navicularis) (fig. 74). The lips of the external meatus project unevenly, the left farther than the right, so that the apex of the glans is asymmetrical (fig. 70A). This asymmetry is due to the presence in the glans of a small penis bone (os penis) which terminates not in the midline, but to the left (fig. 74). An os penis is found in all catarrhine monkeys. It is a bony prolongation of the corpus cavernosum penis into the excavated interior of the glans. The tunica albuginea of the corpus fuses with its periosteum and it is united to the cavernous tissue (trabeculae corporis cavernosi) by fibrocartilage (fig. 74). The glans contains, besides the os penis, a well-developed, independent body of cavernous tissue (corpus cavernosum glandis) (fig. 74).

The prepuce consists of loose folds of skin surrounding the penis behind the collum glandis (fig. 70A).

THE POSITION OF THE PENIS. The penis of catarrhine monkeys, including the macaque, differs from that of man in that, instead of being pendulous from the lower border of the symphysis, it runs forward on to the abdomen for a variable distance. It is relatively fixed, so that only the extreme caudal end of the penis is pendulous. In the rhesus macaque the penis undergoes fixation by the skin as far as the cranial border of the symphysis (fig. 71).

THE FEMALE GENITALIA

THE UTERUS. The rhesus macaque possesses a uterus simplex. The organ is slightly flattened anteroposteriorly. It is divided into a bulbous body (corpus uteri) and a relatively thick-walled cervix, the two being separated by a moderate constriction (fig. 75). Normally the body of the uterus is not anteflexed; instead the axes of uterus and vagina form practically a straight line. The fundus may show a certain degree of separation by a shallow median groove into two cornua. The cervical segment of the uterus is relatively large and conspicuous. The infravaginal segment (portio vaginalis cervicis uteri) is a well-marked protuberance with a transverse, slit-like orifice which is situated towards the anterior border of the cervix, so that the posterior lip (labium posterius) is approximately twice as thick as the anterior one (labium anterius). Moreover, the posterior fornix is deeper than the anterior one. The internal configuration of the cervix is unusual. On examining grossly a medial sagittal plane through the cervix, it is seen that the cervical canal (canalis cervicis uteri) is curiously bent (fig. 76). From the uterine cavity the cervical canal runs slightly posteriorly for a third of its length; it then bends at a right angle following a further course obliquely in an anterior direction. At the level of the infravaginal portion of the cervix the canal enters a sort of vestibule which proceeds caudally to open into the vagina as a slit-like external os (orificium uteri) upon the anterior margin of the cervix. It is the walls of this vestibule which constitute the infravaginal portion of the cervix, composed of a broad posterior and of a narrow anterior lip. The vestibular cervical recess is filled with grossly visible mucus.

THE LIGAMENTS OF THE UTERUS. The *broad ligament* (ligamentum latum uteri) attaches to the uterus by a narrow, membránous attachment along the lateral border (fig. 75). Laterally its two layers deviate from one another and pass over on to the pelvic wall. One layer passes in front around the bladder, the other behind around the rectum. The *round ligament* (ligamentum teres uteri) attaches to the anterolateral surface of the uterus relatively far caudally (fig. 75). This ligament, consisting of smooth muscle and connective tissue, is somewhat flattened. Due to its mode of attachment to the anterior surface of the uterus, it is enfolded in a membranous duplication or extension from the broad ligament. The round ligament can be traced as a stout flattened cord which enters the inguinal canal. The broad ligament continues above into a stout ligament (*ligamentum suspensorium ovarii*), as well as into the *mesovarium* and the *mesosalpinx*.

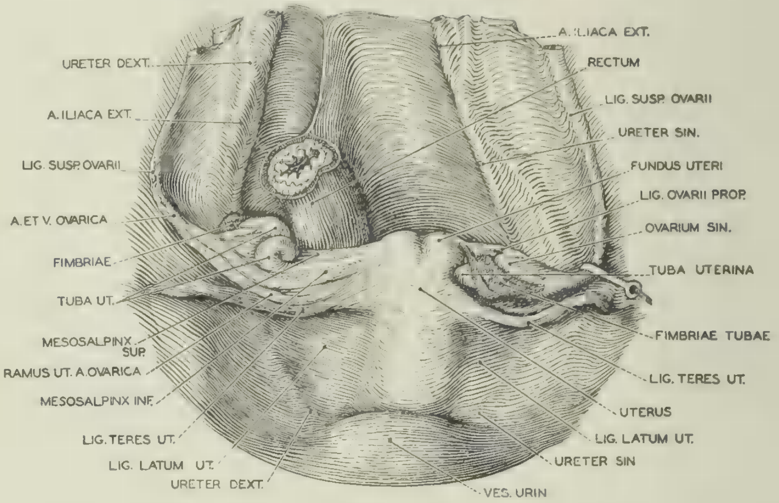

FIG. 75. The pelvic organs of an adult female.

The uterus is relatively extensively covered by peritoneum. The peritoneum clothes recesses (excavatio vesico-uterina and excavatio rectouterina (Douglasi)) situated anteriorly and posteriorly between bladder and uterus and rectum and uterus respectively (fig. 76). These recesses descend to an equal level on the two aspects of the uterus, their apices lying at about the beginning of the infravaginal segment of the cervix. The uterine artery coursing in the broad ligament reaches the uterus in the region of the cervix. After giving off branches to the vagina and cervix, it courses along the lateral border of the uterus, giving off numerous short, penetrating branches.

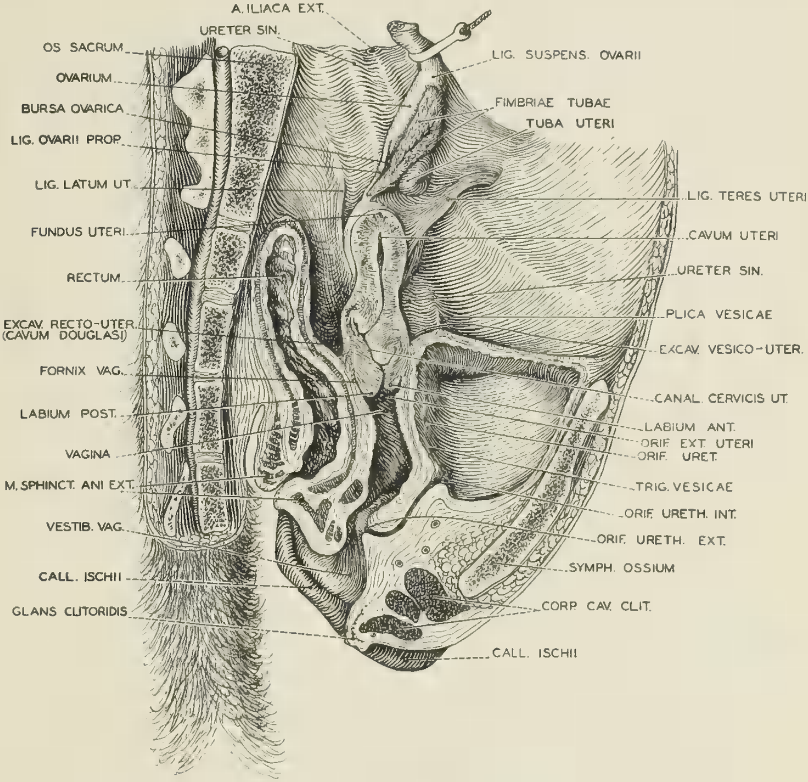

Fig. 76. Midsagittal view of the pelvic organs of an adult female.

The uterus does not lie precisely in the midsagittal plane of the body. Instead, due to a reciprocal relationship with the rectum within the confines of the pelvis, it is usually pushed somewhat to the left, whereas the rectum lies on the right (fig. 75).

The uterine or fallopian tubes. The Fallopian tube (tuba uterina) is relatively convoluted (figs. 75, 76). It possesses well-developed fimbriae which form about the tubal ampulla a compact mass of lenticular shape, with a slit-like orifice. The two ends of the fusiform orifice are composed of a fimbria ovarica and a fimbria uterina, both of them well-defined and of about equal length.

The tube is supported by a delicate inferior mesosalpinx, as well as by a membranous reduplication of peritoneum running along its free border, a superior mesosalpinx. The latter does not exist in man or the great apes. There is formed a deep ovarian bursa (bursa ovarica) which encapsulates the ovary, more or less according to the stage of the menstrual cycle (Westman). There is in a healthy animal a considerable deposit of fat in the inferior mesosalpinx.

THE OVARIES. The ovaries are oval or fusiform in shape, and rest upon the posterior layer of the broad ligament (figs. 75, 76). They are placed at a variable distance from the uterus, to which each is attached by its lower pole by a stout, considerably flattened ligament (ligamentum ovarii proprium). Each ovary is attached along its straight anterior margin to the mesovarium. On the free posterior margin near the upper pole the fimbria ovarica is attached. From the upper pole a strong band (ligamentum suspensorium ovarii), a continuation of the broad ligament, courses upward towards the kidneys. In this ligament are contained the ovarian artery and vein (vasa ovarica). The latter is plexiform.

THE VAGINA. The vagina is a muscular, thick-walled cavity extending from the cervix to the orifice of the vagina and communicating with the vestibule (vestibulum vaginae) (fig. 76). The mucosa is thrown into low longitudinal folds. Besides these, there is in the inner two-thirds of the vagina a multitude of small transverse plicae. In animals which have born young these markings become much obliterated. The longitudinal folds pass over on to the external os of the cervix, especially pronounced on the anterior cervical lip, and pass into the cervical vestibule, where they produce a series of low ridges. At the vaginal orifice there is a constriction and a thickening of the mucosa possibly analogous to a hymen.

THE EXTERNAL GENITALIA. The *vestibule* (vestibulum vaginae) is a funnel-shaped, relatively deep recess (fig. 76). In man, on the contrary, it is much shallower. It opens externally close to the anus beneath the tail, flanked laterally by the ischial callosities. The main axis of the vestibule departs at an obtuse angle from the axis common to the vagina and uterus (fig. 76).

The urethra enters the vestibule at its junction with the vagina (fig. 76). The *external urethral orifice* (orificium urethrae externum) is guarded by two papillary folds. Due to the depth and funnel-like character of the vestibule, the urethral meatus is relatively concealed from the exterior. It is possible, however, with the aid of a small speculum, to insert a catheter into the urethra in the living monkey. In figure 77, drawn from an embalmed specimen, the rima pudendi has been spread apart in order to show the urethral orifice.

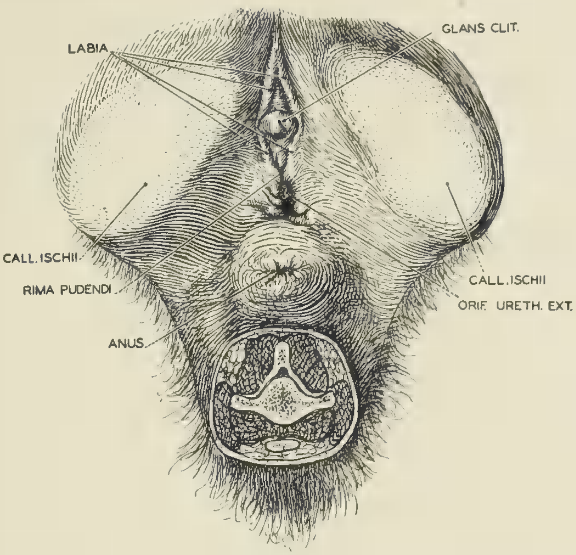

Fig. 77. External genitalia of a female. The rima pudendi has been spread apart in order to show the urethral orifice.

The *rima pudendi* is an irregular slit with puckered edges. At its anterior border is the rather large clitoris (figs. 76, 77). The *clitoris* consists of two crura arising from the ischia, of a body, and of a glans which has a shallow cleft on its under surface. Abundant and well-developed erectile tissue (corpora cavernosa clitoridis) is present.

Bordering the rima pudendi and surrounding the clitoris are rather poorly developed folds or *labia*, analogous probably to the labia minora (fig. 77). The labia unite in front of the clitoris to form a praeputium clitoridis, while behind the clitoris there is no distinct frenulum. The presence of labia majora and of a mons is usually denied for catarrhine monkeys. In the macaque their occurrence is doubtful. In healthy females at puberty, however, there develops a sharply demarcated, thickened area of skin, pigmented, puckered and highly colored, which extends forward over the symphysis like a triangle, with its apex at the pudendal cleft. This area, according to Hartman, is swollen at the time of puberty and has underlying it, to either side of the midline, round masses which can be rolled under the skin. It corresponds closely in extent and position to the scrotal area of the male and may be, therefore, analogous to labia majora and mons which are otherwise lacking in the macaque. The structure under discussion is, moreover, undoubtedly a specialized portion of the area designated as the "sexual skin" by Langley and Sherrington (see chapter III).

Ischial callosities. The ischial callosities (callositates ischiorum) are two areas of thickened, cornified skin which are hairless, and which occur in both sexes (fig. 77). They lie symmetrically over the ischial tuberosities and are not connected in the midline. Between them lie the external genital structures. The anus lies just posterior to the vestibule, separated from it by an extremely short perineum. The anus protrudes and is surrounded by a well-developed sphincter muscle (m. sphincter ani externus).

THE PELVIC MUSCULATURE. The musculature of the pelvic floor and of the perineum and their relationships are described in Chapter VII and illustrated in figure 39.

PLACENTATION. The placenta of the macaque is, as a rule, double discoidal as in the majority of platyrrhine and catarrhine monkeys. The blastocyst implants centrally in the uterine cavity by attaching first either to the posterior or anterior wall of the uterine cavity, usually the latter. This becomes the primary placenta towards which the body stalk is oriented. At a little later stage, as the blastocyst enlarges, it establishes, except in rare instances, contact with the opposite uterine wall, leading to the formation of a secondary placental mass. The umbilical cord attaches to the primary placental disk, the opposite disk being supplied secondarily with blood by vessels that reach it from the primary disk. The placenta, as in the entire group of the Simiae, is deciduate and hemochorial.

Gestation. The gestation period in the rhesus monkey varies between 149 and 180 days, the average duration being 164 days. In the United States the months from October to January constitute the optimum time for conception; the summer months in general constitute the non-breeding season (Hartman). As a rule the fertile period of the menstrual cycle falls between the ninth and the twentieth day of the cycle (Hartman). Pregnancy manifests itself by leakage of blood from the vagina during the third week after mating. This has been designated as the "placental sign" (Hartman).

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CHAPTER XII

THE VASCULAR SYSTEM

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HEART

The heart as a whole, when viewed from the front, presents an elongated oval outline (fig. 78). The right ventricle, like a dilated tube, lies clasping the left ventricle, and pursues a spiral course upward and forward, ending in the pulmonary artery. When filled, this right side is much more prominent than the left. Each ventricle has an apex. The left is the larger of the two, and a broad shallow interventricular sulcus spirals between them on the anterior surface. Of the two atria, the right is much the larger, and both come well to the front, clasping the pulmonary artery by their auricular appendages (fig. 78).

Structurally the two ventricles differ greatly. The septum and the whole of the left ventricular wall are unusually developed, being 7–9 mm. thick. The columnae carneae of the left ventricle are, with two exceptions, much finer and more reticulate than those of the right side. The exceptions are two large massive columns, one each on the anterior and posterior walls of the ventricle, to which are attached most of the chordae tendineae. The right ventricle has a very thin wall, being only one millimeter thick near the apex and 3 mm. thick in the infundibulum. The columnae, however, are larger and more numerous than on the left side and are more irregular in pattern, as in man. The walls of both atria are also very thin and free of folds or ridges except in the auricular appendages. The venae cavae enter the right atrium relatively somewhat more widely separated than in man. Four pulmonary veins (fig. 78) enter the left atrium, the left pair being much larger than the right.

The atrioventricular valves are subject to greater variation than in man. In one instance only two cusps were found on the right side, and in another, four. The valves of the aorta and pulmonary artery are, however, quite uniform and constant. The sinuses of Valsalva in the pulmonary artery are large and well developed, but are less marked in the aorta.

Of the vessels to the heart wall those on the left side are much more highly developed than those on the right. The left coronary artery (*a. coronaria sinistra*) is much larger than the corresponding right vessel, and immediately after leaving the left anterior sinus it divides into its two main divisions, the left circumflex and the anterior descending arteries (fig. 78). These are distributed chiefly to the posterior and anterior surfaces of the left ventricle. The right coronary artery (*a. coronaria dextra*) leaves the right anterior sinus of the aorta, and passing to the right of the pulmonary artery, is distributed to the lateral surface of the right ventricle. The veins of the heart are located chiefly on the left side and primarily on the posterior surface. Here several large vessels may be found coursing upward to empty into the coronary sinus. This vessel is short but rather large in diameter and may receive, as in one example, a patent vein of Marshall. The sinus opens into the right atrium just in front of the opening of the inferior vena cava and is guarded by a well developed thebesian valve. No eustachian valve is found here, however.

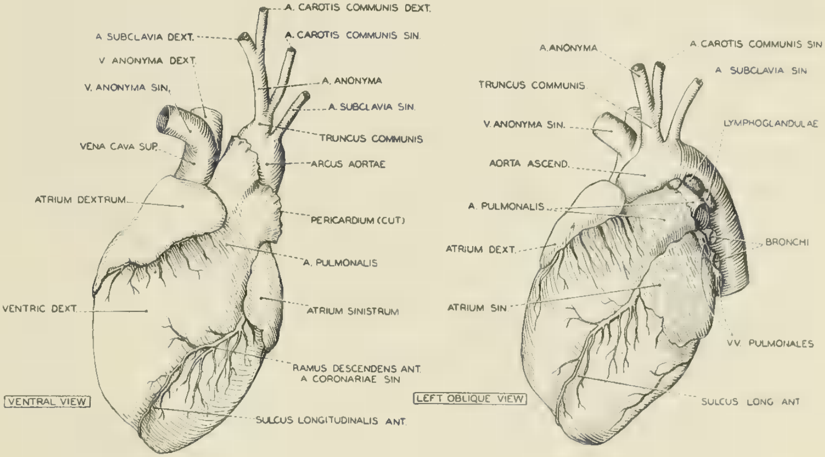

FIG. 78. The heart.

ARTERIES

AORTA. The aorta passes away from the heart by a sharp curve down into the mediastinum in an almost direct anteroposterior plane. In its course through the mediastinum it gives off segmental pairs of branches to the intercostal spaces on the two sides. From its arch only two branches arise. The second and smaller of these, the left subclavian artery (*a. subclavia sinistra*) arises from the crest of the arch and courses directly upward for a considerable distance to emerge from the thorax over the first rib. The first branch, the *truncus communis* (figs. 78, 79) is much larger, and arises from the arch just outside of the attachment of the pericardium. It is a large trunk, 12–15 mm. long, and has no normal counterpart in man. This truncus communis is commonly found in many primates, and it may occur as a variant in man. From it in the rhesus macaque there arise the left common carotid (*a. carotis communis sinistra*) and the innominate (*a. anonyma*). The latter passes back to the vicinity of the right first rib, where it divides into the right common carotid (*a. carotis communis dextra*) and right subclavian (*a. subclavia dextra*). From here the subdivisions are similar on the two sides and will be presented in one description.

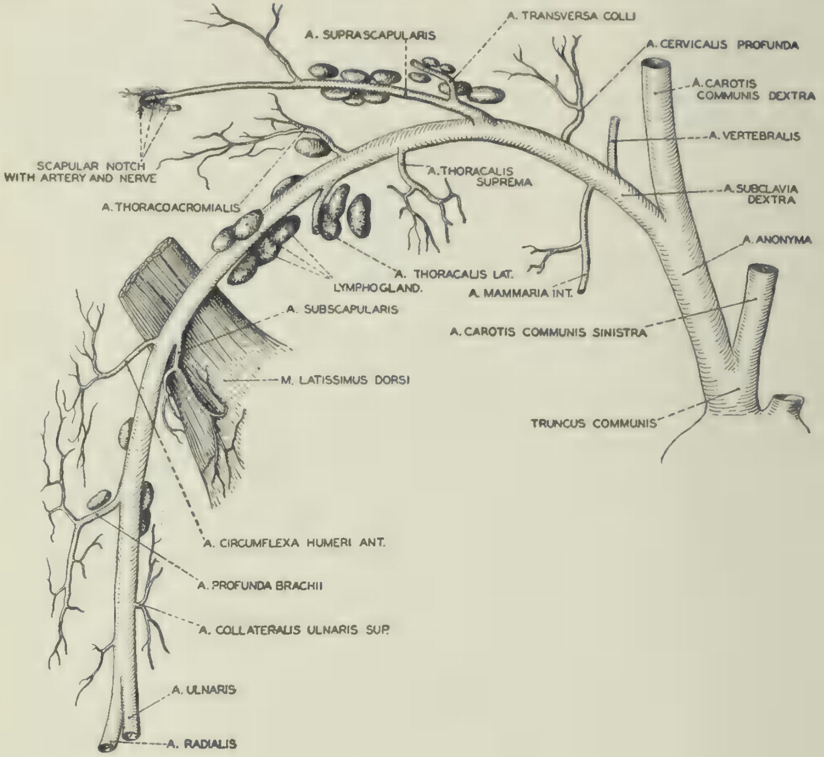

Fig. 79. The right subclavian, axillary and brachial arteries and their branches.

Subclavian artery. Shortly after the subclavian artery leaves its source it gives off the vertebral branch (*a. vertebralis*) (fig. 79), which courses upward and disappears beneath the longus colli muscle into the sixth transverse cervical foramen. The deep cervical (*a. cervicalis profunda*) closely follows the vertebral and runs to the lower deep part of the neck. The suprascapular branch (*a. suprascapularis*) comes next, and from it may spring inferior thyroid, muscular and transverse cervical (a. transversa colli) branches. Its main division, the transverse scapular, passes through the suprascapular notch (fig. 79), above the nerve, and becomes the infraspinous artery. It gives off muscular, articular and anastomotic branches. The internal mammary branch (*a. mammaria interna*) arises from the under side of the subclavian and courses down the mediastinum along the border of the sternum. In its course it gives off a branch to the thymus and one to each of the intercostal spaces, and just before piercing the diaphragm it sends a short communicating branch to its fellow on the opposite side.

Axillary artery. Passing beyond the first rib the subclavian becomes the axillary artery and lies covered by the pectoral group of muscles. From it there arise several branches. The *thoraco-acromial* comes first and is distributed by its two parts to the thoracic wall (a. thoracalis suprema) and acromial region (a. thoraco-acromialis). Occasionally the two vessels may have separate points of origin from the axillary artery (fig. 79). The lateral thoracic (*a. thoracalis lateralis*) is second and is distributed to the thoracic wall lower down. The *subscapular* next leaves on the median side and passes along the lower border and behind the latissimus dorsi muscle. The *anterior circumflex* branch takes origin on the lateral side and runs laterally into the upper arm region.

Brachial artery. In its course down the arm the brachial artery (fig. 79) lies on the median border of the biceps muscle. It gives off only a few branches, the chief one being the *profunda brachii*, which is the main artery to the upper arm. A little lower down, the superior ulnar collateral branch (*a. collateralis ulnaris superior*) is given off. This is a rather large vessel which is the chief supply to the inner side of the lower arm. At the junction of the middle and lower thirds of the upper arm the brachial artery may frequently divide into its terminals, the superficial brachial and ulnar (a. ulnaris) arteries.

Radial artery. Of the two terminals of the brachial artery, the superficial brachial is the larger and more prominent, giving off the greater number of branches about the elbow: muscular, articular, and *radial recurrent*. It passes, as the *radial* artery, beneath the biceps fascia and courses along superficially to the wrist. In the fore arm the radial gives off only a few branches—a nutrient and several muscular—and as it passes the wrist a few articular and communicating branches may arise (fig. 80). In this region a rather large branch is sent over laterally to the dorsum of the hand to be distributed to this region and to anastomose with perforating branches of the palmar arch. From this

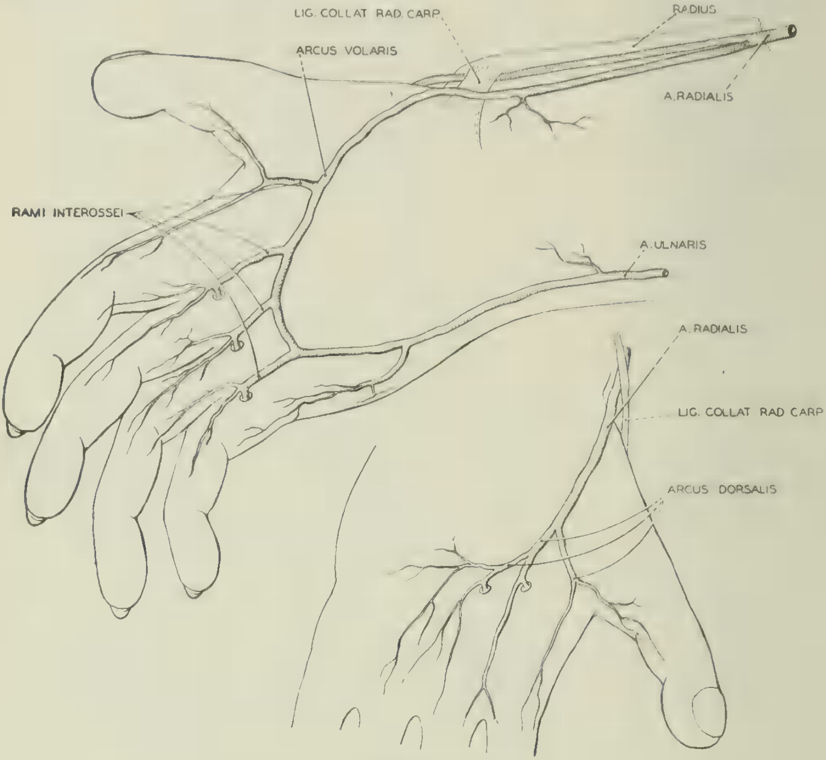

Fig. 80. The volar and dorsal arterial arches.

dorsal vessel (*arcus dorsalis*) a rather constant branch is given off to the thumb and first interosseous space. As it passes beyond the wrist the radial artery courses superficially over the base of the first metacarpal bone and deep to the thenar muscles. It then swings in a long curve across the distal ends of the metacarpal bones, over to the ulnar side, where it units with the ulnar artery and so forms the palmar arch (*arcus volaris*) (fig. 80). There is no other arch, so this one probably corresponds to the superficial arch of man. In crossing the palm it gives off five branches: The first in the first interspace is distributed to the adjacent sides of the thumb and index finger, the second in the second interspace is distributed to the second and third fingers, and so on to the fourth branch and interspace. The fifth branch arises from the ulnar artery and is distributed to the outer side of the little finger. Perforating branches pass through the interspaces and anastomose with similar branches of the dorsal artery.

Ulnar artery. The ulnar artery passes across the elbow joint into the fore arm and disappears beneath the flexor carpi radialis and palmaris longus muscle. Just before doing so, however, it gives off the *anterior interosseous* branch, and in most instances the *dorsal ulnar recurrent* artery. The *inferior ulnar recurrent* branch, which usually arises from the radial artery, may have its origin from the ulnar artery. The interosseous artery usually runs as far as the wrist, giving off small muscular and communicating branches. The main ulnar artery gives off only a few muscular and articular branches, and after passing medial to the pisiform and hamate bones joins the radial artery to form the single palmar arch (fig. 80). The fifth palmar arch branch to the side of the little finger arises from the ulnar artery just beyond the hamate bone.

Common carotid artery. The common carotid artery (figs. 78, 79) passes well into the upper neck region before it divides into its external and internal branches (fig. 81).

External carotid artery. The external carotid (a. carotis externa) passes to about the level of the mandible, where it divides into two large branches. The first of these, the external maxillary (*a. maxillaris externa*), passes forward horizontally and disappears deep to the body of the mandible. Just before it does so it sends downward a branch which in turn gives off a superior thyroid branch (*a. thyroidea superior*), several middle thyroid branches, and some three or four terminal branches to the thyroid cartilage and trachea (fig. 81). Hidden deep to the body of the mandible the main vessel gives off the small *ascending palatine* artery and the lingual artery (*a. lingualis*), the latter much the larger. It then swings under the edge of the mandible and, becoming superficial, is finally distributed to the face. In its course up across the face it gives off the *submental* artery to the region of the chin, and, a little higher up, another branch, which runs to the mouth and divides into the *superior and inferior labial* vessels. The terminal branches are distributed to the nose and the inner angle of the orbit. The second of the two main branches of the external carotid artery passes vertically upward just behind the edge of the mandible and deep to the parotid gland. In its course it gives off the internal maxillary artery (*a. maxillaris interna*) which passes forward into the pterygoid and maxillary regions. The *middle meningeal* artery arises from this vessel as its chief branch. The posterior auricular branch (*a. auricularis posterior*) passes backward to be distributed to and behind the ear. The main vessel continues further upward and ends in the superficial temporal (*a. temporalis superficialis*) and transverse facial (*a. transversa faciei*) branches. All of these vessels lie deep to the parotid gland and finally come from beneath this structure before ending in their terminal regions.

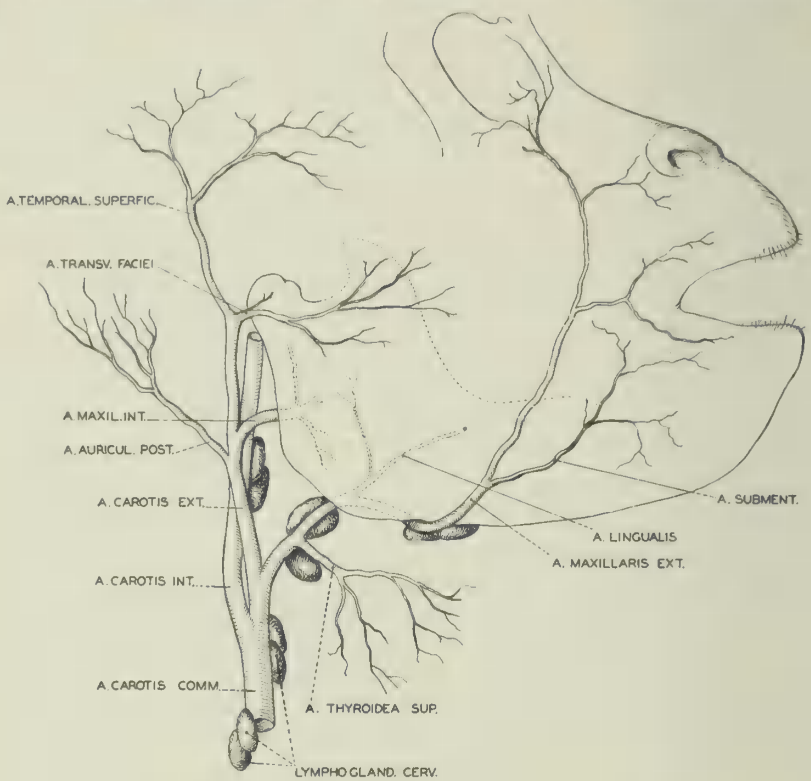

Fig. 81. The right external carotid artery and its branches.

Internal carotid artery. This artery, the smaller of the two carotids, passes deeply up to the base of the skull, where it disappears into the cranium through the carotid canal. Once within the cranium it terminates in the cerebral and the ophthalmic arteries. The *ophthalmic* artery gives off muscular and recurrent meningeal branches, the central artery of the retina, the lacrimal artery, long and short ciliary arteries, anterior nasal and supra-orbital terminals. The *cerebral* arteries are very similar to those of man. The middle and anterior cerebrals are the final endings of the internal carotid artery. The two vertebrals, after passing into the cranium through the foramen magnum, join on the ventral surface of the medulla near the pons and form the *basilar* artery. From this vessel there are given off the posterior inferior cerebellar, the anterior inferior cerebellar, the superior cerebellar, the internal auditory and pontine branches. The posterior cerebral artery is the terminal of the basilar and from it arises the posterior communicating union between it and the middle cerebral. The anterior communicating union, a short trunk joining the two anterior cerebrals, completes the *circle of Willis*, as in man (fig. 95).

ABDOMINAL AORTA. Passing down through the thoracic mediastinum the aorta sends segmental branches to the intercostal spaces and finally enters the abdomen through the aortic opening in the diaphragm to become the abdominal aorta (aorta abdominalis) (fig. 82). Here it gives off the following branches, a few small vessels to the under side of the diaphragm, then the larger visceral trunks.

COELIAC AXIS. This (a. coeliaca) is a rather large trunk (fig. 82) which in turn gives off (1) the splenic artery (*a. lienalis*), a rather small but distinct vessel which sends a small branch to the omentum just before entering the spleen, (2) the left gastric (*a. gastrica sinistra*), a much larger vessel which sends branches to the fundus and greater curvature of the stomach and several small branches to the spleen, ending at the pylorus by turning down into the omentum and right colon, and (3) the right gastric (*a. gastrica dextra*) which passes along the lesser curvature of the stomach and ends by dividing into the gastroduodenal and hepatic (a. hepatica) arteries. The first of these is distributed to the pyloric end of the stomach and the duodenum, while the second enters the liver through the portal fissure. Just before entering the fissure it gives off the small cystic artery (a. cystica) to the gall bladder.

SUPERIOR MESENTERIC ARTERY. The superior mesenteric artery (a. mesenterica superior) (fig. 82) leaves the aorta just caudal to the coeliac axis and enters the broad enterocolic mesentery. The main branches of the artery are distributed to the small intestine and the greater length of the colon in long primary and secondary arches.

Inferior mesenteric artery. This vessel (a. mesenterica inferior) arises from the abdominal aorta some distance below the coeliac and is distributed to the lower end of the colon (figs. 82, 83). One branch turns headward along the gut and anastomoses with colic branches from the superior mesenteric, the others pass caudalward and supply the gut for its remaining length. Some nine or ten branches originate from this artery and present several peculiarities. They scale downward in length from the first, several centimeters long, to the last, only a few millimeters in length. In addition to being successively shorter they are gradually spaced closer together. The first two divide about midway, and from these branches secondary arches may form, especially in the region of the first. All the others divide a centimeter or two short of the intestinal wall and form only primary arches (fig. 83).

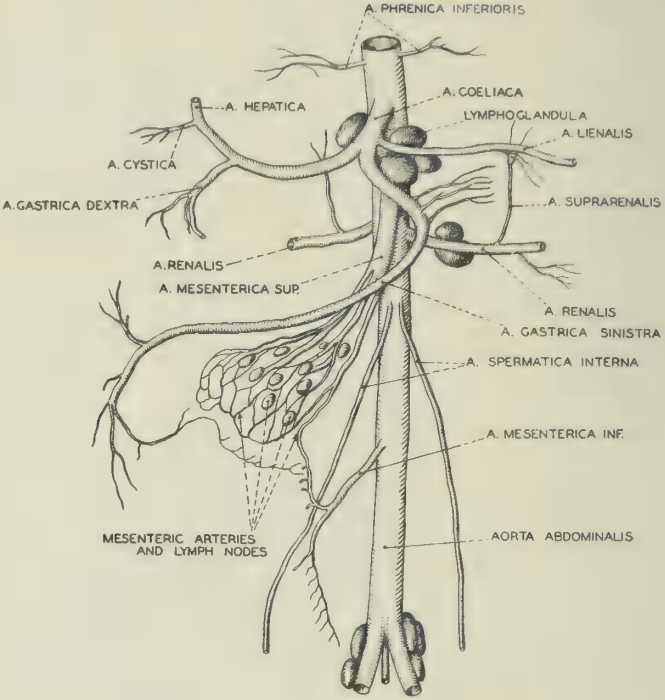

Fig. 82. The abdominal aorta and its branches.

Renal arteries. These vessels (aa. renales) leave the aorta laterally and run directly to the kidneys on either side (figs. 82, 84). Just before entering the kidney each gives off a branch to the suprarenal gland of its side (for further details and variations see chapter XIII).

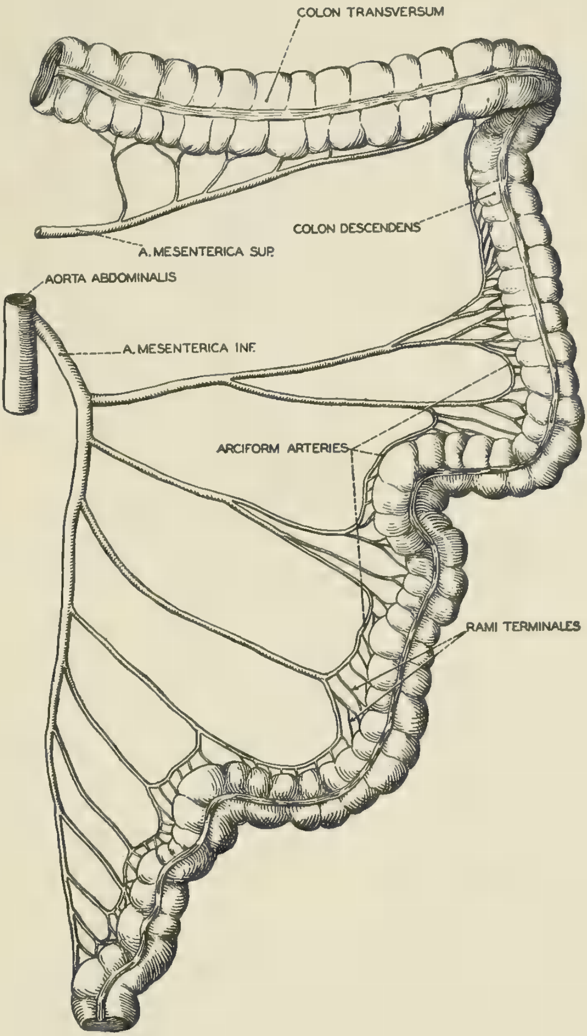

Fig. 83. The superior and inferior mesenteric arteries and their branches.

Spermatic (or ovarian) arteries. These two vessels arise separately from the anterior surface of the aorta and follow a long independent course to the testicles or ovaries (figs. 39, 71, 82). Small segmental vessels spring from the dorsolateral surface of the aorta and enter the lumbar interspaces.

COMMON ILIAC ARTERIES. In the lower lumbar region the aorta divides into its terminals, the common iliac arteries (figs. 39, 82, 85). This vessel (a. iliaca communis) shortly divides into the external iliac (a. iliaca externa) and the hypogastric (a. hypogastrica) arteries (figs. 39, 82, 85).

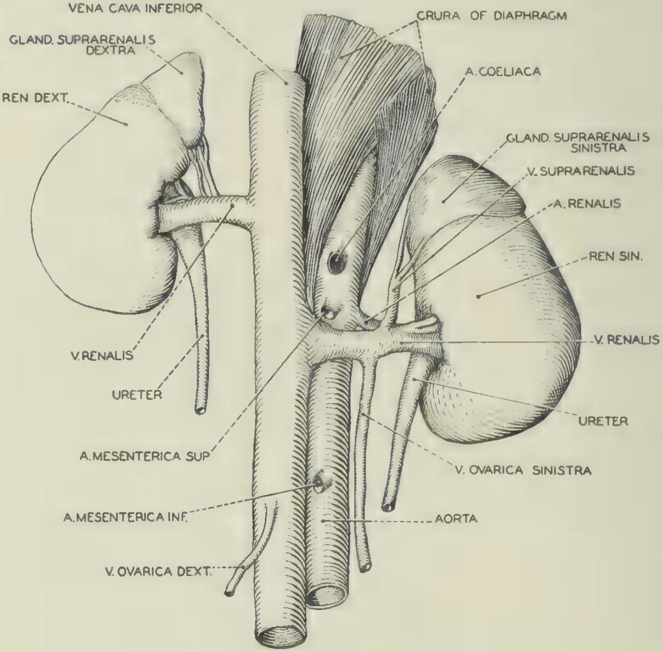

FIG. 84. The blood vessels of the kidney.

HYPOGASTRIC ARTERY. This turns sharply into the pelvis and gives off a number of branches. These include a small *vessel to the ureter*, a *lateral sacral*, a *uterine*, the *superior and middle vesicular*, and several *branches to the fundus and base of the bladder* (figs. 69, 85). The *gluteal* artery leaves the pelvis through the greater sciatic foramen and is distributed to the gluteal region (fig. 85). The *pudendal* artery also passes through the same notch, but under cover of the piriformis muscle, and is accompanied by the pudendal nerve (fig. 85). It then swings under the obturator internus muscle and enters the perineum, which it supplies.

The *obturator* artery passes out of the pelvis through the obturator foramen and is distributed to the upper inner region of the thigh (figs. 39, 85). The *medial circumflex femoral* artery is commonly a branch of the obturator, but may arise from the hypogastric. It passes forward and disappears beneath the inguinal ligament medial to the psoas muscle and is distributed to the regions of the lower abdomen and upper thigh (figs. 39, 85).

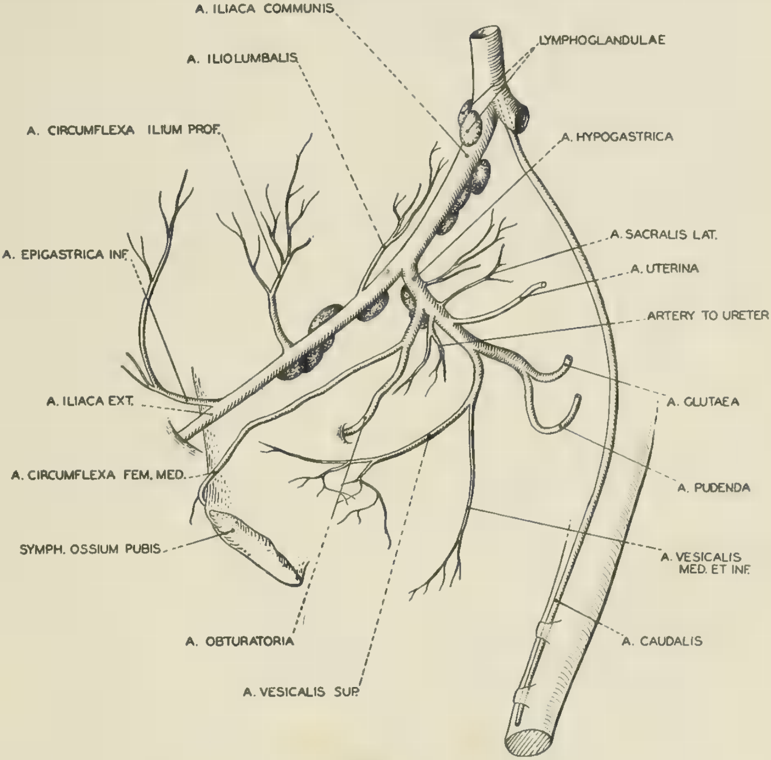

FIG. 85. The right common iliac artery and its divisions, the hypogastric and externa iliac arteries.

EXTERNAL ILIAC ARTERY. The other division of the common iliac artery, the external iliac (a. iliaca externa), courses along the rim of the pelvis and gives off the iliolumbar (*a. iliolumbalis*), the deep circumflex iliac (*a. circumflexa ilium profunda*), and the *inferior epigastric* branches (figs. 39, 85). It then passes into the thigh (figs. 39, 85) and becomes the femoral artery.

FEMORAL ARTERY. This vessel passes toward the knee under cover of the sartorius muscle and gives off the following branches: The superficial circumflex iliac (*a. circumflexa ilium superficialis*), which is distributed to the upper anterior region of the thigh, and the *profunda femoris*, which in turn gives off the lateral circumflex and muscular branches to the median region of the thigh (fig. 86). In the thigh the femoral artery divides into its terminals, the saphenous (*a. saphena*) and popliteal (a. poplitea) arteries. The former (which occurs in many primates and occasionally in man) gives off the highest genicular (*a. genu suprema*) branch and then passes between the sartorius and gracilis muscles; it courses down the median border of the tibia to its lower third, where it turns sharply and crosses over to the anterior surface of the bone (fig. 86). It then passes under the transverse crural ligament and becomes the deep dorsal pedal artery (*a. dorsalis pedis profunda*). In the foot it swings across the tarsal bones to join a branch of the posterior tibial below the lateral malleolus. In its course it gives off several small branches to the lower leg region and just distal to the ligament it commonly gives off branches to the second, third and fourth spaces. These interosseous branches pass through or send communicating branches to the plantar region; a few small branches are given off from the original vessel to the dorsum of the foot just before it passes around behind the lateral malleolus. A large vessel usually arises from the saphenous well up in the leg and courses independently down to the first interspace superficial to the transverse crural ligament as the superficial dorsal pedal artery (*a. dorsalis pedis superficialis*) (fig. 86). Just before reaching the first interspace it sends a fair sized branch around to the plantar surface. The main vessel, now reduced, passes through the interspace to the plantar region. A few branches from it are distributed to the great and second toes on their dorsal surfaces. The second of the divisions of the femoral, the *popliteal* artery, passes posteriorly between the heads of the gastrocnemius muscle to the back of the leg (fig. 86). In its course it gives off a number of branches, muscular, articular and nutrient; one usually pierces the interosseous membrane and becomes the anterior tibial (*a. tibialis anterior*) artery, which does not reach the foot, however. The original vessel then continues downward as the posterior tibial artery (*a. tibialis posterior*) and swings below the internal malleolus into the sole, where it is distributed to the planta by several branches. Shortly after passing around the malleolus it divides into its medial and lateral plantar terminals (fig. 86). The former (*a. plantaris medialis*) is the larger,—it courses along the median border of the foot, turning near the distal end of the first metatarsal bone to run to the lateral side. In this curve it forms union with the dorsal pedal arteries in the first, second and occasionally the third interspace. It also sends small branches to the plantar region of the toes. The lateral plantar artery (*a. plantaris lateralis*), though smaller than the medial, gives a more

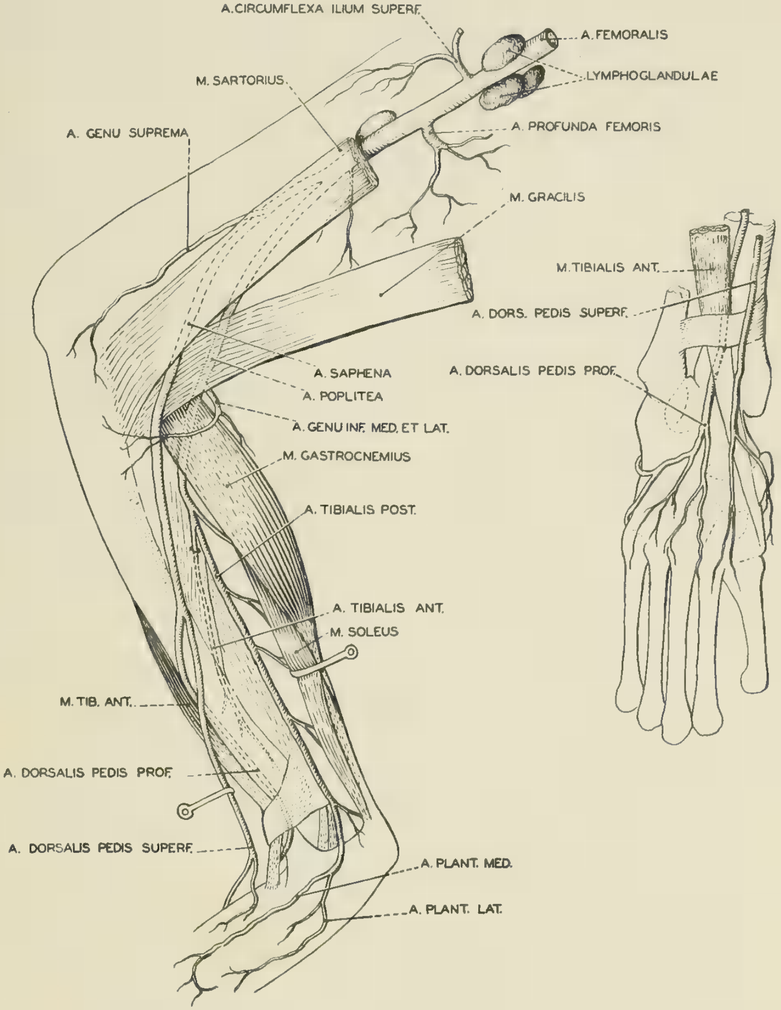

FIG. 86. The right femoral artery and its branches. The insert shows the arterial supply of the dorsum of the foot.

plentiful distribution of branches to the sole. It is terminal, but it may anastomose occasionally with the medial artery, a plantar arch thus being formed.

Caudal artery. The caudal artery (a. caudalis) is an unpaired vessel that arises from the posterior surface of the abdominal aorta close to its terminal bifurcation (figs. 39, 82, 85). It passes along the anterior surface of the sacrum with two venae comites and disappears into the tail through the anterior vertebral arches (chevron bones).

VEINS

Superior vena cava. The superior vena cava (vena cava superior) is relatively much longer than in man, but is similarly composed of the combined innominates and the azygos vein (figs. 61, 78). The *azygos* vein is made up of tributaries from the third thoracic to the upper lumbar posterior segmental veins on the right side. It courses upward through the mediastinum slightly to the right, and curving over the root of the right lung joins the vena cava. At about the level of the sixth vertebra it receives the *hemiazygos* vein from the left side. This vessel, composed of the lower thoracic and upper lumbar segmental tributaries, pursues a lateral vertebral course, passing to the right side and joining the azygos vein. The *superior hemiazygos* vein is composed of the posterior intercostal veins of the third, fourth and fifth, and occasionally the sixth, left interspaces, and drains into the hemiazygos vein. Occasionally it passes by a separate vessel across to the azygos vein. The veins of the first and second left interspaces combine, and the single vessel empties into the left subclavian vein. On the right side the first, and occasionally the second, segmental vein empties into the right innominate vein.

Innominate veins. The two relatively long innominate veins (vv. anonymae) unite just to the right of the midline and form the large but short vena cava. Followed laterally the innominate is seen to receive the external and internal jugular (*vv. jugularis externae et internae*) and the subclavian veins (*vv. subclaviae*) (figs. 61, 81). The external jugular vein receives the *superficial cervical* and *transverse scapular* veins, as well as several small muscular veins. Higher up in the neck it receives a connection from the anterior facial vein (*v. facialis anterior*). This vessel drains the infra-orbital, nasal, labial and mental regions, but the main drainage is into the internal jugular vein. The chief tributaries of the external jugular are the posterior auricular (*v. auricularis posterior*), superficial temporal (*v. temporalis superficialis*) and internal maxillary (*v. maxillaris interna*) veins. The *internal jugular* vein carries the main flow from the face and the intracranial region. Within the cranium the chief tributaries are the cavernous and lateral sinuses. Other tributaries of the innominate vein are the internal mammary vein, mediastinal veins and the thoracic duct.

Subclavian vein. The subclavian vein (fig. 61) receives the *cephalic*, *basilic* and *brachial* veins. These vessels are extremely variable, but in the main they are similar to those of man. The superficial vessels of the fore arm and hand are very sparse, since the main drainage is through the venae comites of the arteries.

Inferior vena cava. The inferior vena cava (figs. 39, 84) is relatively much longer than in man, as is the superior vena cava, and, like it, has a composition similar to its human counterpart. As it passes by the liver it is nearly surrounded by the caudate lobe; in this vicinity it receives a number of small tributaries (*vv. hepaticae*), primarily from the right lateral lobe and right side of the central lobe. A little higher up it receives two rather large tributaries, a right and a left, draining the left portion of the gland. Commonly these two fuse into one and this single vessel then enters the vena cava. In any case, the right vessel drains the major portion of the central lobe, chiefly from the left and center, and the left one drains the left lateral lobe (fig. 67). This left hepatic vein frequently drains an area from the left diaphragm. The tributary vein passes downward and to the right through the left triangular ligament and joins the left hepatic vein some distance before this vessel enters the vena cava.

The chief tributaries of the vena cava, in addition to these hepatic vessels, are the renal (figs. 68, 84) and common iliac (fig. 39) veins. The *renal* veins are comparatively small and they drain, in addition to the kidney proper, the capsule and the suprarenal gland. There may be several vessels of this last group or only one relatively large vein (cf. chapter XIII for variations). On the left side the *spermatic* (or ovarian) vein enters the renal (fig. 84). This is a small but constant vessel draining the testicle (or ovary) and enters the renal on its caudal side. On the right side, however, the similar vessel enters directly into the vena cava. Just before doing so it may receive the capsular veins, several in number, from the right kidney. More remotely the vena cava receives, through the *common iliac* veins (fig. 39), tributaries from the pelvis and the extremities. These in the main follow the arteries as venae comites, as in the upper extremities. In the leg and foot, however, the *long saphenous* vein is more constantly present.

Portal vein. The portal vein is quite similar to its counterpart in man, being composed of gastric, splenic, superior and inferior mesenteric veins. The *gastric* veins drain chiefly the pyloric region; a few tributaries are received from the capsule of the liver. The *splenic* vein is small but prominent and receives a few small tributaries from the greater curvature and fundus of the stomach. The *superior mesenteric* veins, several in number, drain up through the mesentery from the small intestine and the first part of the colon and are in direct communication with a rather isolated group of veins in the lower colic area, the inferior mesenteric veins. These vessels drain into one rather large isolated trunk, the *inferior mesenteric* vein, which empties into the general mesenteric trunk, higher up. A number of very small vessels may be found draining the under surface of the diaphragm into the hepatic veins. On the left side these may be organized into one fairly large vessel, as before mentioned.

LYMPHATICS

Both lymph nodes and lymphatic vessels are poorly developed in the extremities, but are large and numerous in the trunk. A few small nodes can be located on the branches of the external maxillary artery, especially about its lingual and superior thyroidal branches (fig. 81). Lower down in the neck the nodes are more numerous and are larger; they are found closely associated with the branches of the subclavian artery (fig. 79). Quite a number of small glands are clustered about the suprascapular artery, and in the axilla the nodes are unusually large. They follow the main branches of the axillary artery and extend with the main artery into the neck. Those about the lateral thoracic branch are usually well developed. In the arm only an occasional small node may be found, as in the trochlear region. Within the trunk the glands are more constant. The tracheal and bronchial nodes are relatively well defined; several large bodies, the superior bronchial, are located on the bronchi near the trachea, and other smaller ones are associated with the subdivisions of the air tubes. Some medium sized bodies are lodged in the turn of the aorta, especially on the left side (fig. 78). In the abdomen the nodes are numerous and large. Surrounding the branches of the superior mesenteric artery there are a number of intermediate sized bodies, and in the region of the coeliac axis three or four large glands are found (fig. 82). In the mesentery the nodes are small but freely distributed even into the colic region. The nodes in the pelvis are numerous and follow the main branches of the arteries (fig. 85); those of the hypogastric artery are large, in some instances completely surrounding the vessel. In the inguinal region the nodes are more variable, but commonly are the largest found in the entire lymphatic system (fig. 86). Lower down in the leg a few small bodies may be found in connection with the arteries, especially in the popliteal space.

THORACIC DUCT. The thoracic duct is a small tube that begins in the upper lumbar region and extends up into the mediastinum, closely following the aorta and emptying into the left subclavian or innominate vein.

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Chapter XIII

THE ENDOCRINE GLANDS

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HYPOPHYSIS (PITUITARY)

(Figs. 56, 87, 93, 95)

The hypophysis on the whole is strikingly similar to that of man, so that the following description will chiefly stress points of difference. Two injected specimens (adult females) and one uninjected male (immature) comprise the basis for the description.

The hypophysial complex consists of the anterior lobe, posterior lobe, and intermediate lobe, and lies deep in the bony cavity, the sella turcica. Posteriorly, the hypophysis is bordered by the wall of the dorsum sellae, which extends upwards and forward to cover the largest part of the posterior lobe and part of the anterior lobe as well. The floor of the sella is not so flat as that of man, but instead is triangular in shape, with the apex extending anteriorly and at a higher level than the base. At the apex of this triangular floor arises a small bony tubercle, the tuberculum sellae, which marks the anterior border of the hypophysis. A slight depression above the tuberculum sellae and superior to the hypophysis marks the channel of the intercavernous sinus.

Laterally, folds of the dura mater separate the hypophysis from the medial wall of the cavernous sinuses, through which run the internal carotid arteries. The lateral folds are continuous in front to form part of the anterior border of the hypophysis and are continuous dorsally over the hypophysis itself. Another heavier dural membrane is located dorsally over the hypophysis, extending from the anterior to the posterior clinoid processes and continuous laterally to form the outer border of the cavernous sinuses. This is the diaphragma sellae. But since the anterior dorsal edge of the hypophysis seems to be at the tuberculum sellae, there exists a space between the diaphragma sellae and the membrane covering the base of the sella turcica anterior to the gland, which is the intercavernous sinus. Thus the hypophysis is completely enclosed in a dural membrane except for the opening made by the stalk where it unites the posterior lobe with the hypothalamus.

The two internal carotid arteries run forward and slightly upward in the cavernous sinuses, converging to a noticeable degree. They make a sharp upward turn and pierce the diaphragma sellae lateral and anterior to the infundibular stalk. The optic chiasma lies slightly anterior and dorsal to the hypophysis.

The hypophysis is ovoid in shape and measures about 3–4 mm. anteroposteriorly, 4 mm. dorsoventrally, and about 6–7 mm. in width. (These measurements are from the 2 adult females weighing about 3.5 to 4 kilograms each.) The anterior lobe can be distinguished by its reddish coloration, an indication of its glandular function, while the posterior lobe is more of the texture of the brain tissue. The anterior lobe is somewhat bean-shaped; the posterior fills the concavity of the hilus. The latter lobe may extend quite far posteriorly into the angle formed by the dorsum sellae and the floor of the sella turcica. The shape of the sella makes this lobe well seated in a bony case, more so than the anterior one. The posterior lobe is attached to the hypothalamus by the short stalk, approximately 2–4 mm. in length. A very small cavity can be seen extending from the lower part of the 3rd ventricle into the stalk itself. The intermediate lobe and pars tuberalis are so small that they cannot be recognized grossly in preserved specimens.

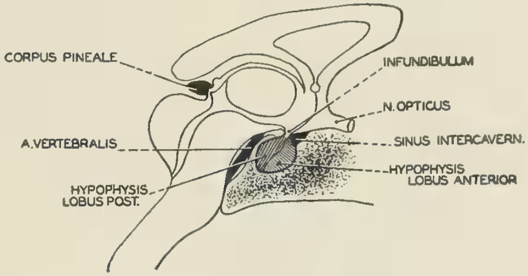

FIG. 87. The third ventricle of the brain with the pineal and pituitary glands.

As to the circulation, little can be said. In one specimen injected with India ink, small vessels could be seen under the binocular microscope extending for the length of the infundibulum as far as the opening through the diaphragma sellae. Their small size precluded any attempt to trace them into the hypophysis itself. Surrounded as the hypophysis is with large arteries and spacious venous sinuses, small or medium sized vessels either to or from the gland are conspicuous by their absence.

PINEAL BODY

(Figs. 87, 93)

The pineal is attached by a broad base to the dorsal posterior border of the thalamencephalon. It is a small conical-shaped body about 2–3 mm. wide at the base and 2–3 mm. long, extending almost horizontally to lie in the furrow between the two superior colliculi. The distal end terminates at the union of the tentorium and falx cerebri. The two habenular ganglia are to be seen lateral and anterior to the pineal. The short thick stalk contains a cavity which is continuous with the third ventricle.

THYROID GLAND

(Fig. 88)

In general structure and position the thyroid of the rhesus monkey is similar to that of man. It is situated at the front and sides of the neck and consists of two lateral lobes connected across the midline by an isthmus. The lobes appear more elongated than in man, and the isthmus is very much narrower. There is no evidence of a pyramidal lobe. The gland is placed high in the neck, the isthmus and bases of the lobes being located at the level of the third tracheal ring and the apices extending superiorly almost to the hyoid bone. From a surface view of the thyroid little idea is gained of its size, as the greater part of the gland is placed at the sides and back of the trachea. This accounts for the narrow appearance of the lobes and for the length of the isthmus across the midline.

The lobes are roughly pyramidal in shape. The right is slightly larger than the left, measurements in the adult female being approximately 9 by 15 mm. and 8 by 14 mm. respectively. The anterolateral surfaces of the lobes are covered by the skin, fascia, sternocleidomastoid, sternohyoid, sternothyroid muscles, and superior belly of the omohyoid. The posteromedial surface rests upon the trachea, cricoid and thyroid cartilages, inferior pharyngeal constrictor and cricothyroid muscles, esophagus, and the common carotid arteries.

The isthmus of the gland measures about 8 mm. in length by 3 mm. in width. In the midline of the neck it is covered by the skin and fascia, and laterally by the sternothyroid muscles.

The thyroid is enclosed in a connective tissue capsule derived from the pretracheal layer of the cervical fascia, which projects into the substance of the gland and divides it into innumerable lobules.

The blood supply of the organ is extensive, especially the venous return. Superior, middle, and inferior veins drain corresponding areas of each lobe; all empty into the internal jugular at varying levels on either side, with the exception of the left inferior vein, which terminates in the innominate behind the sternum. The superior veins come from the apices and medial surfaces of the lobes and form an anastomotic connection from either side along the upper border of the isthmus. The inferior veins arise from the posterior surfaces and drain the bases of the lobes and the lower border of the isthmus; the middle vessels drain the rest of the lobes posteriorly. There is but one artery, from the external carotid, penetrating the apex of each lobe at the hyoid level. In the rhesus monkey there is apparently no vessel corresponding to the infe-

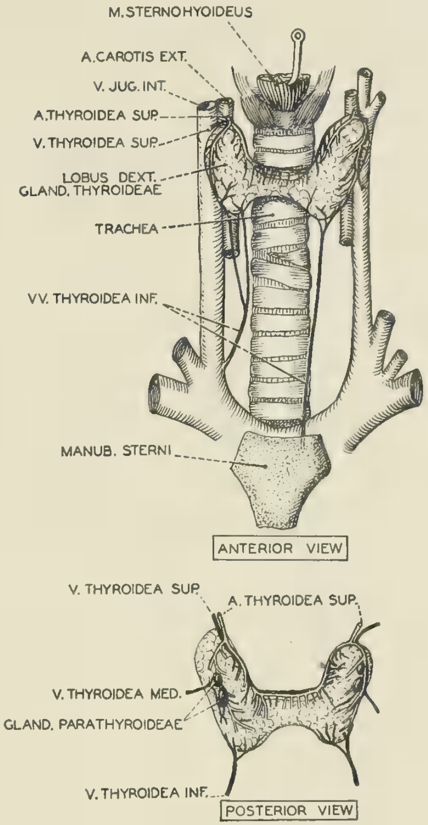

Fig. 88. A typical thyroid gland, with its blood supply.

rior thyroid artery of the human. At its point of entry the artery divides into anterior and posterior branches, which supply the two surfaces of the lobe; the anterior divisions of each side send anastomosing branches across the upper border of the isthmus.

The sympathetic nerve supply of the thyroid is very extensive—from the lower cervical ganglia—forming a plexus-like network around the medial posterior surface of the gland.

PARATHYROID GLANDS

(Fig. 88)

The parathyroids of the rhesus monkey are four minute reddish bodies. Two are applied to the posterior surface of each thyroid lobe and are barely distinguishable from their substance. The glands are more spherically shaped than in the human and relatively larger (in comparison with the size of the thyroid lobes). They are also less adherent to the surface of the thyroid, each pair being partially enclosed in its own connective tissue sheath. The individual glands are closely paired on either side, rather than at the extremities of the thyroid lobes, as in man. Each pair is situated at the point of division of the middle thyroid veins, the right being at a higher level than the left.

ADRENAL (SUPRARENAL) GLANDS

(Fig. 89)

The adrenals of the rhesus monkey bear the same relation to the kidneys, in both size and position, as do the corresponding organs of man. They are flat, pinkish bodies placed above the upper pole of each kidney, on the posterior abdominal wall behind the peritoneum. The two glands differ in morphology and relationships on either side.

The right adrenal is shaped like a flattened wedge and in the adult measures about 20 by 10 mm. along its greatest axes. It is situated behind the right lobe of the liver and lateral to the inferior vena cava; the base rests upon the upper end of the kidney, and the apex is shaped to the curve of the diaphragm. The upper lateral portion of the anterior surface is in relation with the bare area of the liver and is devoid of peritoneum. Both the anterior and posterior surfaces are flattened, for the ridges of the wedge are located laterally, rather than anteriorly, as in man.

The left adrenal is in the shape of a flattened pyramid. It is slightly broader than the right gland, measuring approximately 20 by 15 mm.

The base of the pyramid rests on the kidney. The anterior surface is in relation superiorly with the cardiac end of the stomach and the upper extremity of the spleen, and inferiorly with the pancreas; the latter area is non-peritoneal. The posterior surface is placed against the diaphragm lateral to the descending aorta as it emerges through the hiatus.

The adrenal glands are more independently situated than in man, at a greater distance from the structures along the vertebral column, and less closely shaped over the kidneys. Each adrenal is enclosed in a fibrous capsule of subperitoneal fascia, of the same structure as the one around the kidney, that contains much fatty tissue and sends numerous processes into the substance of the gland.

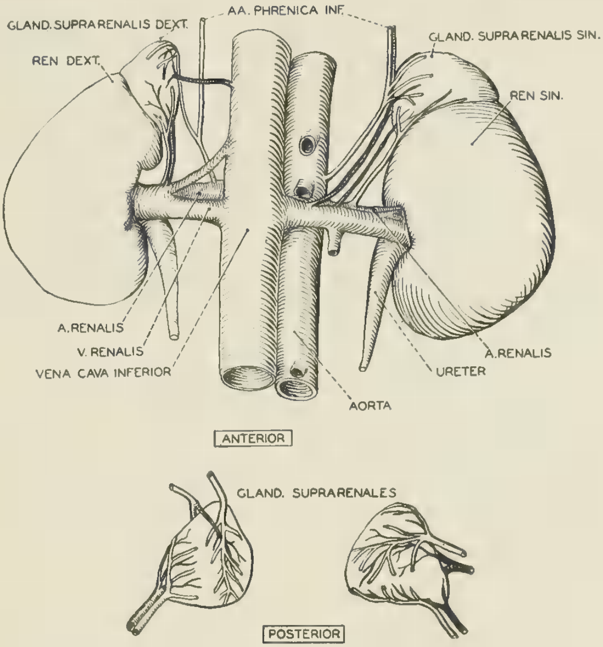

Fig. 89. The adrenal (suprarenal) glands with their blood supply.

The sources of blood supply of the organs differ somewhat from those in man. The arteries are small and several in number, arising from the inferior phrenics and renals on either side. They penetrate the adrenal capsule posteriorly along the medial border and separate into anterior and posterior divisions. The branches from the inferior phrenic artery furnish the main supply for the superior portion of the gland, while those from the renal supply the inferior portion. The venous drainage comprises one large vessel and several small ones on either side. On the right the large vein emerges from the capsule posteriorly and empties into the inferior vena cava; on the left side it terminates in the renal vein. These vessels, through anterior and posterior branches, form the principal drainage of the superior portions of the glands. The inferior portions are drained by the small veins, which empty into the renals. Since the adrenals of the rhesus monkey are at a greater distance from the arterial and venous trunks along the midline, branches from the latter to the glands are relatively longer than in man.

The nerve supply of the organs is very extensive, comprising a network of sympathetic strands from the coeliac and renal plexuses. Branches of the phrenic nerves in the vicinity also appear to penetrate the capsule.

THYMUS GLAND

(Fig. 90)

The thymus undergoes changes similar to those in man, but at a relatively more rapid rate. It apparently increases in size from birth to about the age of one year, when it ceases to grow and gradually atrophies, until in the adult it has almost completely disappeared.

At the height of development the organ consists of a mass of greyish tissue situated in the region of the superior and middle mediastina. It is imperfectly divided into lobes and lobules, of which a cervical and two lateral divisions are the most prominent. The right lateral lobe measures approximately 35 by 15 mm., the left lobe 30 by 18 mm., and the cervical portion 10 by 8 mm.

The lateral lobes rest upon the surface of the pericardium behind the sternum and costal cartilages and spread over the roots of the great vessels; laterally they are bounded by the mediastinal pleura. They cover the region of the right atrium and left auricle, the right ventricle, and two-thirds of the left ventricle anteriorly, and enclose the greater part of both atria posteriorly. The longer right lobe extends to the level of the 6th costal cartilage, the left as low as the 5th costal cartilage. The broader left lobe overlaps the right along the midline.

The cervical part of the gland is a continuation of the larger lateral portions from the superior mediastinum to the level of the 6th tracheal ring. It rests upon the front and sides of the trachea, over the origins of the cervical vessels, and is covered by the sternohyoid and sternothyroid muscles. Cervical prolongations of the lateral lobes also extend posteriorly behind the great vessels, especially around the junction of the left internal jugular and subclavian veins.

The thymus gland, as a whole, is enclosed in a thin fascial capsule that separates its divisions from the surrounding structures in the neck and thorax.

The arteries of the thymus are short branches from the internal mammaries of both sides just after their origin from the subclavian trunks. The thymic arteries penetrate the organ in the superior portions of the lateral lobes and divide to supply the anterior and posterior surfaces of the various parts of the gland. The veins are more numerous than the arteries. Those draining the cervical portion empty posteriorly into the inferior thyroid vessels, and those from the lateral lobes into the internal mammaries on both sides, while a large vein arises from the posterior surface of the gland at the junction of the cervical and lateral lobes, to terminate in the left innominate trunk.

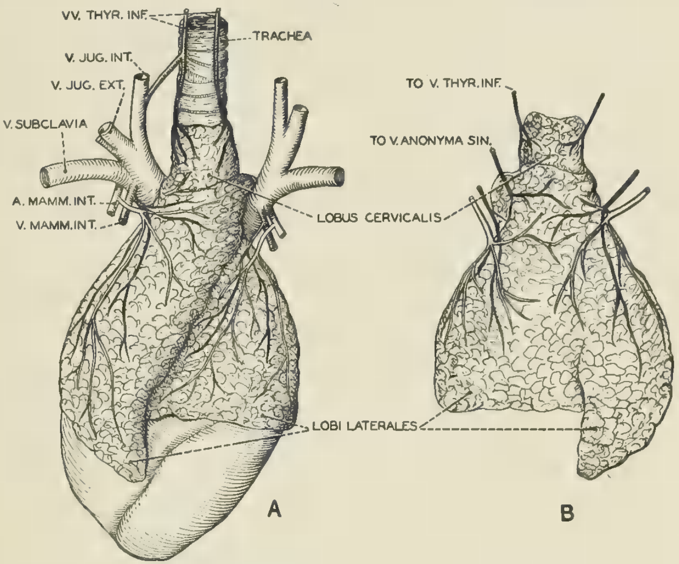

FIG. 90. The thymus of a yearling monkey, and the blood supply of the gland. A, ventral view; B, dorsal view.

The nerve supply of the thymus consists of numerous small twigs from the vagus and sympathetic trunks in the lower part of the neck. Furthermore, in relation to the organ a large group of lymph glands is situated on each side around the point of division of the thymic branches from the internal mammary vessels. These glands apparently drain the thymus and communicate with the larger inferior deep cervical group.

The above description applies to the monkey of 5 to 7 months of age. In the newborn the thymus is less developed, covering a smaller area of pericardium over the ventricles. In the adult animal it has become reduced to a slight accumulation of fatty tissue in the superior mediastinum, occasionally supplied by a few branches from the internal mammary vessels.

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Chapter XIV

THE EXTERNAL MORPHOLOGY OF THE BRAIN AND THE SPINAL CORD

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This study of the brain and spinal cord of *Macaca mulatta* is of necessity confined to a consideration of external structure, checked, where the data are available, by internal configuration. Consequently, when more is known about the microscopic anatomy of the brain of this animal, the identification and comparison of certain morphological peculiarities must be modified.

THE CORTEX CEREBRI

The telencephalon is easily divided into the four lobes typical of the mammalian brain. On the lateral surface the fissura centralis (f. cent., figs. 91, 92) divides the frontal lobe from the parietal. Anterior to this fissure lie two others, the sulcus precentralis inferior (s. prec. i., figs. 91, 92) and the sulcus precentralis superior (s. prec. s., figs. 91, 92). Passing anteriorly between the curve of the former sulcus lies the fissura principalis (f. princ., figs. 91, 92), in old terminology, the sulcus rectus. The fissura principalis separates the gyrus frontalis medialis (g. fr. m., figs. 91, 92) from the gyrus frontalis inferior (g. fr. i., figs. 91, 92). That part of the dorsolateral surface which lies anterior to the gyrus precentralis (g. prec., figs. 91, 92) and medial to the sulcus precentralis superior has been called the gyrus frontalis superior (g. fr. s., fig. 92).

Posterior to the central fissure lies the gyrus postcentralis (g. postc., figs. 91, 92), the most anterior gyrus of the parietal lobe. Ventrally this gyrus is bounded by the deep sylvian fissure, the fissura lateralis (f. lat., figs. 91, 92), which hides the Insula. This fissure continued in a dorsoposterior direction often converges with the sulcus temporalis superior (s. temp. s., figs. 91, 92). Between them lies the superior temporal gyrus (g. temp. s., fig. 91), and ventral to this sulcus the gyrus temporalis medius (g. temp. m., fig. 91) is found. Below the most ventro-anterior angle of this gyrus a short indentation in the cortical surface is always present. This identation might be called the inferior temporal sulcus (s. temp. i., fig. 91) because a short gyrus, the gyrus temporalis inferior (g. temp. i., figs. 91, 95), can be seen between it and the fissura collateralis. Such an identification is strengthened by the fact that beneath a similar fissure in *Cercopithecus* Brodmann (1909, p. 151) has identified an area 20 which is directly homologous with the cyto-architecture found in the anterior part of the inferior temporal gyrus of the human brain.

The lateral surface of the occipital lobe probably extends ventral to the sulcus occipitalis inferior (s. oc. i., figs. 91, 94) and anterior to the sulcus lunatus (s. lun., figs. 91, 92). For again the cyto-architectonic studies of Brodmann discovered that both of these fissures bisect area 18 of the occipital lobe in *Cercopithecus* and that area 19 is extended a short distance ventrally and anteriorly to area 18. Such a finding would mean that the more dorsal part of the middle temporal gyrus could not belong to the temporal lobe, but rather to the occipital. The smooth surface of the area striata (17) which composes the greater part of the lateral surface of the occipital lobe is unbroken by fissuration in the particular brain used for illustration, although the writer has seen in some brains of this species, especially those of five year old animals, a fissure, whose position is indicated in figure 91 by the dotted line, sulcus occipitalis superior.

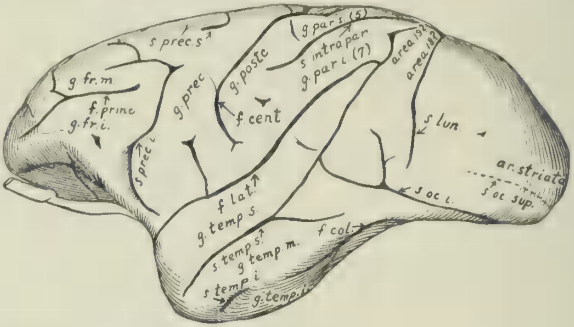

FIG. 91. Lateral view of left cerebral hemisphere.

The medial surface of the anterior division of the telencephalon is broken by a deep fissure, the sulcus callosus marginalis (s. cal. mar., figs. 93, 94). Dorsal to this sulcus the medial division of the gyrus frontalis superior (g. fr. s., fig. 93) and the paracentral lobule of the motor cortex are found, while ventral to the sulcus in question lies the gyrus callosus marginalis (g. cal. mar.). This fissure is a real boundary, because neither area 4 nor area 6 extends ventral to it. And the cytoarchitecture of the gyrus callosus marginalis ventral to both area 4 and area 6 is that of a typical granular cortex. Between the ventro-anterior part of the corpus callosum (c. c., fig. 93) and the sulcus rostralis (s. rost., fig. 93) lies the gyrus callosus (g. cal., fig. 93).

The fissuration at the posterior pole of the medial surface is marked by the presence of the fissura calcarina. In monkeys this fissure is divided into an anterior and a posterior division (f. cal. p. and f. cal. a., figs. 93, 94) and is not joined as in higher primates by the fissura parieto-occipitalis (f. or s. par. oc., figs. 92–94). That fissure is here an independent one, which runs over the crest of the cortex to join the sulcus intraparietalis (s. intrap., fig. 92) and the sulcus lunatus (s. lun., fig. 92). Dorsal to the calcarine fissure is found the cuneus, and ventral to that fissure the gyrus lingualis (cu. and g. ling., fig. 94). Passing ventrally

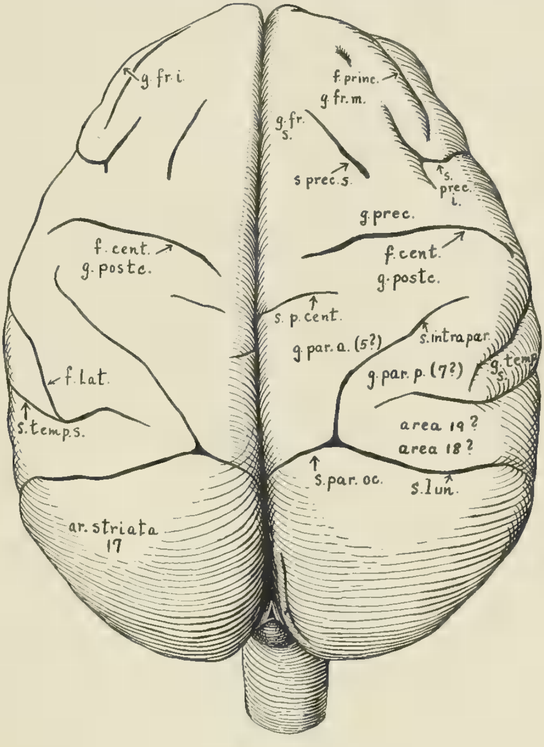

Fig. 92. The brain from above.

from the gyrus lingualis a deep fissure is discovered, the fissura collateralis (f. col., fig. 94). The fissura collateralis may or may not become confluent with a small fissure crossing the face of the gyrus lingualis. This confluence in some brains of this species may join the calcarine fissure. Between the fissura collateralis and the sulcus occipitalis inferior lies a gyrus which may be homologous to the gyrus fusiformis of man (g. fus., fig. 94). The boundary between the gyrus lingualis and the gyrus hippocampus cannot be determined by any surface markings. Only a cyto-architectonic study of this region could determine that line. All that can be said is that the gyrus hippocampus, bounded laterally and anteriorly by the fissura rhinalis (f. rh., figs. 94, 95), turns dorsoposteriorly in typical fashion to form the uncus (unc., fig. 94).

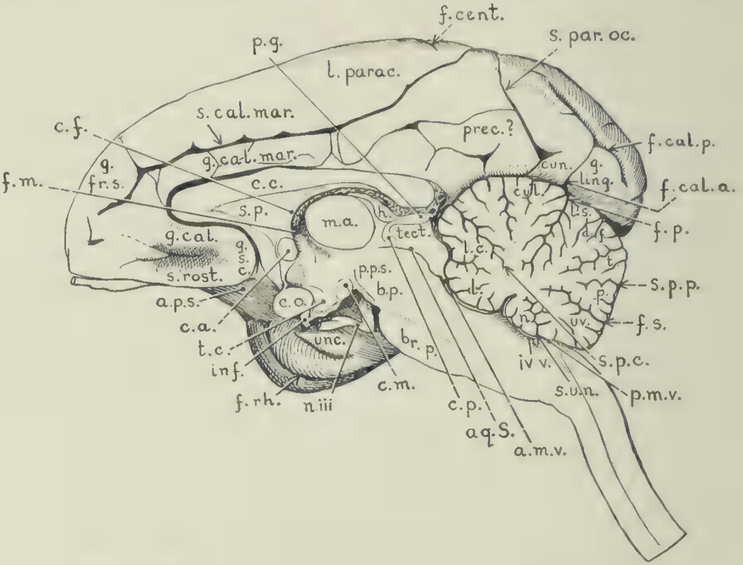

FIG. 93. The brain in midsagittal section (mesial surface).

The anterior boundary of the parietal lobe is the fissura centralis, its lateral margin the fissura lateralis, and its posterior limit an imaginary line joining the confluence of the fissura lateralis and of the sulcus temporalis superior and the sulcus parieto-occipitalis. On the medial surface it extends caudalward as far as the sulcus parieto-occipitalis and cephalward probably beyond the dorsoposterior limb of the sulcus callosus marginalis. The line of ventromedial delimitation cannot be placed with any precision, because, firstly, the writer has been unable to determine any homology for the fissure (not labelled in either figs. 93 or 94) which is found dorsal and caudal to the splenium of the corpus callosum, and, because, secondly, the cyto-architecture of this region is not known. Were it comparable to *Cercopithecus*, the fissure in question would mark its ventral limit, and the posterior limb of the sulcus callosus marginalis would not. Possibly the triangle formed by these fissures and the parieto-occipitalis is the precuneus. Although the fissura centralis in some brains passes over the crest of the telencephalon into the medial surface, Bucy (1933) has found that in this region, that fissure does not mark the posterior limit of the motor cortex. The Betz cells are absent for a distance of several millimeters anterior to this part of the fissura centralis (f. cent., fig. 93).

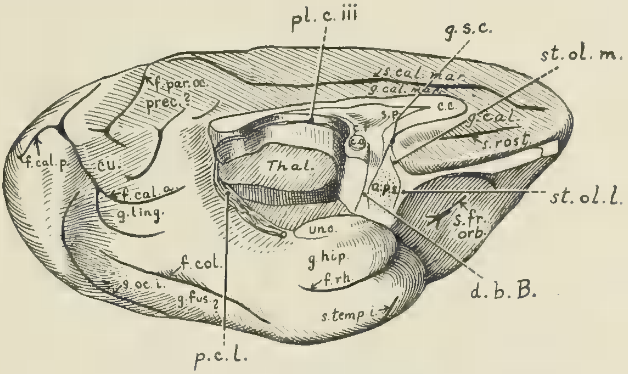

FIG. 94. Oblique median view of left cerebral hemisphere after removal of the brain stem.

The region between the sulcus intraparietalis and the confluence of the lateral fissure and the sulcus temporalis superior has been called the gyrus angularis, although it is well known that the histological structure which characterizes that gyrus in man has never been identified in monkeys. Rather, this region is area 7 of Brodmann, and therefore the writer has labeled it the gyrus parietalis posterior. Its structure is similar to that of the posterior division of the superior parietal lobule in man. Again the area which lies cephalward of the dorsal part of the sulcus intraparietalis (s. intrapar., fig. 92) and the sulcus parieto-occipitalis has been named the gyrus parietalis anterior for similar reasons (g. par. p., and g. par. a., fig. 92). The sulcus postcentralis (s. p. cent., fig. 92) probably marks the caudal boundary of the postcentral gyrus.

The lateral surface of the frontal lobe is separated from the orbital or ventral division by the sulcus fronto-orbitalis (s. fr. orb., figs. 94, 95). The orbital division contains two gyri, the gyrus rectus and the gyrus orbitalis, separated by the sulcus orbitalis (g. rec., g. orb., s. orb., fig. 95). The nervus olfactorius (n. ol., fig. 95) covers a part of the gyrus rectus. And similar to other primates this nerve is divided into a visible lateral and a medial stria (st. ol. m., and st. ol. l., fig. 95). The lateral stria disappears from view beneath the uncus and the medial stria can be followed with the aid of a hand lens into the gyrus subcallosus (g. s. c., figs. 93, 94). Passing from the medial to the lateral olfactory areas is the flattish diagonal band of Broca (d. b. B., fig. 94). In the trigone formed by this band and the two stria, the anterior perforated space is found (a. p. s., fig. 94).

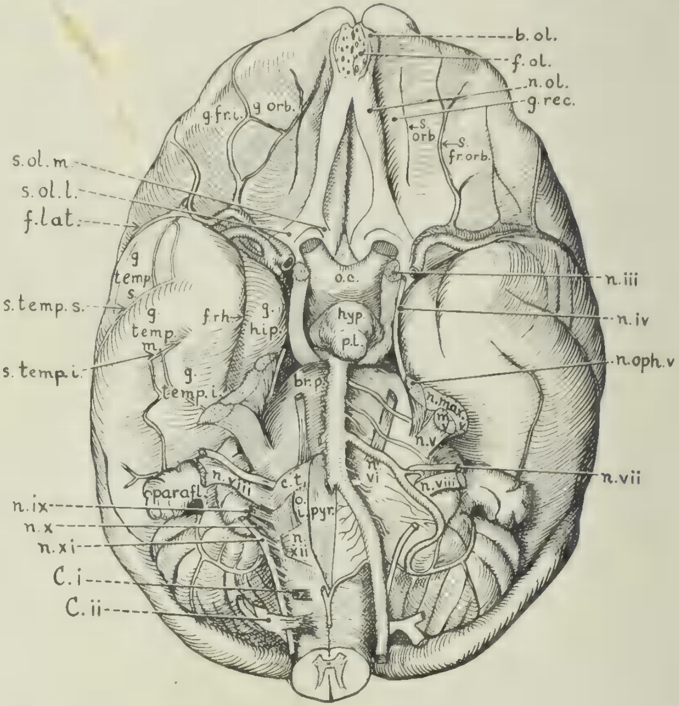

FIG. 95. Base of brain. The blood vessels have been partly dissected away on the right side.

THE CEREBELLUM

The medial sagittal section (fig. 93) of the cerebellum of this macaque shows the typical division into three lobes by a deep anterior fissure, the fissura prima (f. p.), and a deep posterior fissure, the fissura secunda (f. s.). The anterior lobe contains the typical subdivisions, the culmen (cul., figs. 93, 96) or parts III and IV of Bolk; the lobulus centralis (l. c., 93, 97), part II of Bolk; and the lingula (l., figs. 93, 97), part I of Bolk. The culmen and the lobulus centralis are separated on the medial surface by the deep sulcus postcentralis (s. p. c., fig. 93), the lobulus centralis and the lingula by the sulcus postlingualis (not labelled in fig. 93).

The medial lobe, using Elliot Smith's posterior boundary, consists of three main divisions; (1) the lobulus simplex, (2) the declive, the folium cacuminis, and the tuber valvulae, and (3) the pyramis (l. s., d., f., t., p., figs. 93, 96). The pyramis is separated from the tuber by the sulcus prepyramidalis (s. p. p., figs. 93, 96). This sulcus was used by Ingvar as the posterior limit of the middle lobe.

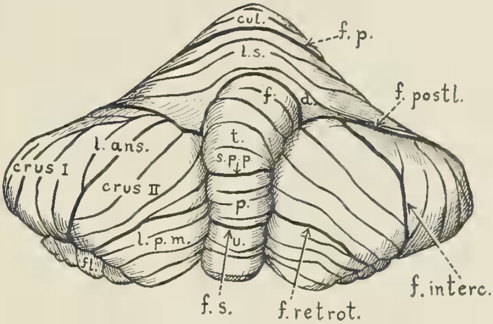

Fig. 96. Posterior view of cerebellum.

The pyramis is separated from the uvula by the fissura secunda (f. s., figs. 93, 96, 97), and the uvula (u.) from the nodulus (n.) by the sulcus uvulonodularis (s. u. n., figs. 93, 97). From the medial surface the anterior lobe appears to be the largest, although not so from the dorsal surface (fig. 96). The lobulus simplex has no lateral projections and in this macaque occupies at least three folia. There is some question whether its posterior limiting sulcus should be placed anterior to the region marked f or to that labelled d. The deep sulcus, which bears the designation of fissura postlunata (f. postl., fig. 96), is morphologically the line of separation between the lobulus simplex and CII of the lobulus complicatus (Bolk), but crus I of the lobus ansiformis (l. ans., fig. 96) is not only attached to the folium cacuminis (f.) but also to the folium anterior to it, which was thought to be the declive (d.). Certainly on the medial surface the sulcus between the lobulus simplex and the declive is deeper than that between the declive and the folium (l. s., d., and f., fig. 93).

Crus I and crus II of the lobus ansiformis are marked by the deep fissura intercruralis (f. interc., fig. 96). Crus I is definitely attached by a slender thread of tissue to the folium and crus II to the tuber. The tuber valvulae is separated from the pyramis by the sulcus prepyramidalis (s. p. p., figs. 93, 96), which can be traced laterally into the hemispheres as the fissura retrotonsillaris (f. retrot., fig. 96). This fissure, which ought to be called pretonsillaris, is the anterior limit of the lobus paramedianus (l. p. m., figs. 96, 97) or the tonsilla (Ingvar). These three lateral components of the lobus ansiformis make up the lateral hemisphere of the cerebellum and are connected medially with Bolk's lobuli CII and CI.

The exact relation of the lateral projections of the lobus posterior to the inferior vermis is rather difficult to determine. One attachment, however, is certain, that of the flocculus (fl., fig. 97) to the nodulus by a slender ribbon of white matter. The flocculus is isolated from the formatio vermicularis (Bolk) and the paraflocculus (Smith) by the fissura flocculo-parafloccularis (f. fl. p. fl., fig. 97), and the formatio vermicularis from the overhanging lobus ansiformis by the fissura parafloccularis (f. p. fl., fig. 97). As far as the writer can determine in the adult the formatio vermicularis (f. verm., fig. 97) is a lateral outgrowth of the pyramis, leaving the uvula without any lateral extensions. Should this probable relationship be proven true by subsequent embryological studies, Ingvar's contention that the dividing sulcus between the middle and posterior lobe is the sulcus prepyramidalis rather than the fissura secunda would have the added weight of a primate condition, already upheld by analysis of the cerebellum of monotremes (Hines, 1929).

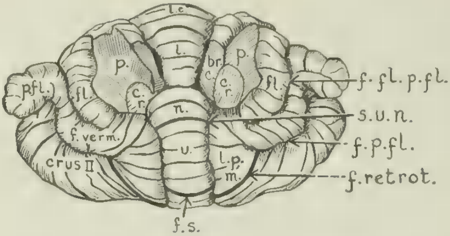

FIG. 97. Ventral surface of cerebellum.

Considered from a comparative point of view the striking aspects of the cerebellum of this primate are the equal division of tissue between crus I and crus II of the lobus ansiformis and the relatively large size of the lobus paramedianus.

THE BRAIN STEM

The medial sagittal section of the prosencephalon reveals three of the usual structures as proportionately large, the anterior commissure, the optic chiasma and the massa intermedia (c. a., c. o., m. a., fig. 93). The tuber cinereum lying between the optic chiasma and the corpus mamillare (c. m.) is a thin walled structure which, directed caudalward, ends in the infundibulum (inf.). The stria medullaris thalami (s. m. th., fig. 98) can only be seen from the medial surface at the place where it enters the habenula (h., fig. 93), which is a large bilateral pyramidal structure. To its most posterior extremity the anterior limb of the pineal gland is attached (p. g., figs 93, 98). The posterior limb of this gland is attached to the roof of the diencephalon at its posterior border, dorsal to the posterior commissure (c. p., fig. 93).

The cut surface of the tectum (tect., fig. 93) and of the basis pedunculi demonstrate that together they occupy approximately two-thirds of the total thickness of the midbrain, leaving the last third for the structures characteristic of the tegmentum. The pons (br. p., fig. 93) is relatively a large structure, although by no means occupying as great a proportion of this region as in the apes or man. The thin veil-like caudal and cephalic attachments of the cerebellum to the medulla, the anterior and posterior medullary vela (a. m. v., p. m. v., fig. 93) can be easily seen as forming the anterior and posterior part of the roof of the fourth ventricle (iv v.).

Looking down upon the dorsal aspect of the brain stem (fig. 98) the large nucleus which bulges medially from the lateral part of the telencephalic vesicle is the nucleus caudatus (n. c.). Posteriorly this nucleus is outlined by the stria terminalis thalami (s. t. th.), beyond which lies an infinitesimal indentation, the di-telencephalic groove (d–t. g.). The dorsal surface of the thalamus is easily delimited into lateral and medial parts. In the medial division the anterior nucleus (n. a. th.) and the medial nucleus (n. m. th.) can be allocated anterior to the habenula (h.), its commissure (c. h.) and its large incoming grouped system of fibers, the stria medullaris thalami (s. m. th.). Immediately posterior to the commissure of the habenula the pineal gland (p. g.) may be seen spread out in a flattish triangular manner, covering completely the region of the posterior commissure. Laterally the contours of the dorsal surface of the thalamus disclose the positions of the lateral nucleus of the thalamus and the pulvinar (n. l. th., and pul., fig. 98). (Those interested in the configuration of this part of the thalamus will find a careful consideration on p. 457 of Mussen's atlas.)

The relative difference in the distribution of tissue between the superior colliculus (c. s.) and the inferior colliculus (c. i.) is not as great as that seen in man. However, the more lateral placing of the inferior colliculus appears to be quite similar. Emerging from behind this latter body is the radix of the nervus trochlearis (n. iv).

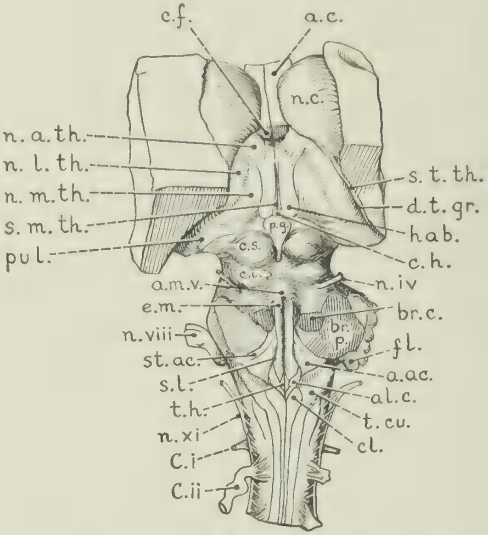

Fig. 98. Dissection of brain stem, dorsal view.

The anterior medullary velum (a. m. v., fig. 98) covers the cephalward part of the floor of the fourth ventricle, attaching itself to the surface of the brain dorsal to the brachium conjunctivum (br. c.). Through this veil two of the typical surface markings of the floor of this trapezoidal space appear, the indentation or midline groove and the lateral groove, the sulcus limitans (s. l., fig. 98). When this sulcus is followed caudally it separates a large triangular area, the area acustica (a. ac.) from a slender hour glass region (eminentia medialis, e. m., fig. 98), which is broken by two smaller lines or hillocks, which inclose respectively the trigonum hypoglossi (t. h.) and the ala cinerea (al. c.). The trigonum hypoglossi covers the more anterior part of the nucleus hypoglossi for its posterior division vanishes from sight beneath the medial approach of the two alae. The ala cinerea as in man marks the position of the dorsal motor nucleus of the vagus.

In the particular brain used for illustration the region of the ala cinerea is marked by two small projections, in others which the writer has studied these hillocks are flattened. Since both of these hillocks are medial to the sulcus limitans, they cover, in all probability, motor regions of some variety. Turning to Geist's study, only the dorsal motor nucleus is pictured and labelled for the entire region. Were this true, then the rhesus macaque would have relatively a larger dorsal motor nucleus of the tenth than any other mammal so far studied. The region lateral to the nucleus of the nervus hypoglossus contains in other mammals besides the nucleus of the vagus, the nucleus intercalatus of Staderini. Further it is not impossible that a part of the dorsal sensory nucleus of the vagus is slightly displaced and occupies a part of the more lateral division of this region.

The more or less even contour of the area acustica is slightly disturbed by stria medullaris acustica (st. ac.), which swings from the lateral aspect of the medulla oblongata around the caudal limit of the pons in a cephalomedial direction to disappear from view into, or in some brains just medial to, the groove of the sulcus limitans. Beneath the surface of the more cephalic part of the medial hour glass area lie the cells of the central gray, uninterrupted at any point by a colliculus facialis (Geist, 1930).

The dorsal markings of the medulla are those typical of primates: The clava (cl.), which is the eminence produced by the nucleus gracilis, and the tuberculum cuneatum, the external ridge formed not so much by the nucleus cuneatus as in man but rather by a nucleus, which Geist (1930) labels, without explanation of its internal relationships, the nucleus externus of Blumenau. The clava and the tuberculum cuneatum extend caudally as two fiber bundles occupying the whole space, in some brains of this species, between the exit of the dorsal roots of the upper two cervical nerves.

On the ventral surface of the brain stem the anterior perforated space is outlined by the striae olfactorius lateralis and medialis and the diagonal band of Broca (st. ol. l., st. ol. m., d. b. B., fig. 99). Projecting ventrally, caudal to this area is the optic chiasma (c. o.), from which project the two optic nerves (n. ii). From the optic chiasma the optic tract (tr. op.) swings dorsally and caudally, lying close upon the lateral surface of the brain stem to end in the corpus geniculum laterale (l. g. b.). The passage of part of these fibers to the superior colliculus cannot be followed by examination of the external morphology of the brain stem.

The tuber cinereum (t. c.) emerges from beneath the optic chiasma, flanked dorsally by the flattish hummocks formed by the corpus mamillare (c. m.). The radices of the nervus oculomotorius (n. iii) emerge medially to the great fiber systems of the basis pedunculi (b. p.). Some of the fibers of the peduncle re-emerge from beneath the brachium pontis (br. p.) as the pyramids (pyr.). In this particular brain the decussation must be almost complete on the left or the few fibers which remain as the uncrossed pyramidal tract do not leave their mark upon the external surface. Lateral to the pyramids the inferior olive bulges outward, often unequally as pictured in figure 99. Dorsal to the olive, a flat band of fibers lying caudal to the brachium pontis, attached laterally to the nervus acusticus, disappears beneath the pyramids, the corpus trapezoideum (c. t., fig. 99). The corpus trapezoideum, together with the stria medullaris acustici (st. ac., fig. 98), embraces the lateral surface of the medulla from either side, but cannot in either case be observed, from examination of the external morphology, to cross the midline. In the brains both of man and of the chimpanzee the corpus trapezoideum is covered by the brachium pontis.

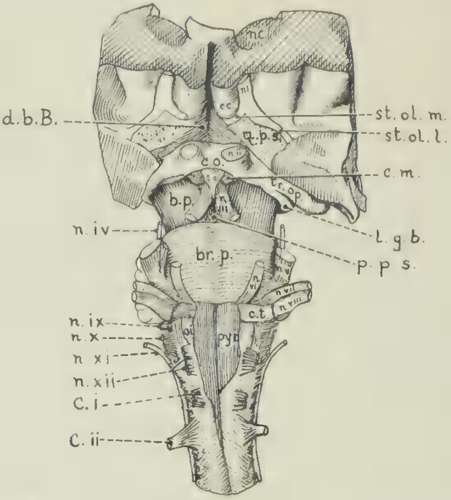

FIG. 99. Dissection of brain stem, ventral view.

The nervus abducens (n. vi) emerges in its typical mammalian manner from beneath the brachium pontis, and the fine fiber radices of the nervus hypoglossus (n. xii) make their exit medially to the medial border of the inferior olive. The roots of the nervus glossopharyngeus and the nervus vagus (n. ix, n. x) leave the medulla in two very slightly separated strands, one more lateral, on a horizontal level with the root of the eighth nerve, and the other strand more ventral, although appreciably lateral to the roots of the twelfth nerve. The nervus facialis (n. vii) and the nervus trigeminus (n. v), leave the medulla on the same sagittal plane, well lateral to the exit made by the sixth nerve. The place of exit of the seventh nerve is found between the caudal border of the brachium pontis and the eighth nerve. No separation of the facial nerve into facial proper and nervus intermedius was observed at this exit. Generally the nervus trigeminus leaves the medulla midway between the caudal and the cephalic borders of the brachium pontis. But in this macaque, its exit is found to be one-third of the total distance from the caudal border. The motor root of this nerve is posterior to its two sensory roots; and the opthalamic division lies medial to the maxillary. Anterior to the transverse plane of the exit of the twelfth nerve, the eleventh nerve (n. xi) receives a few nerve fila. Not only at the levels of emergence of each of the upper cervical nerves (C_1 to C_4) does the eleventh nerve receive filamentous contributions, but also between them, very small fibers have been observed joining the main trunk of the nerve.

THE SPINAL CORD

The total number of spinal nerves is given by Howell and Straus (chap. XVI, this book) as 34, i.e. 8 cervicals, 12 thoracics, 7 lumbars, 3 sacrals and 4 caudals. In the particular specimen which the writer dissected only 33 could be found, there being 3 rather than 4 caudal nerves.

Caudal to the second cervical nerve no ridges or furrows can be observed on the surface of either the dorsal or the ventral funiculus. The outer contour of the spinal cord to the naked eye is smooth. This smoothness, so unlike the ridging present on the dorsal and ventral surfaces of the human spinal cord, is not the only feature of difference between the two. The greatest lateral diameter occurs in this macaque at the sixth and seventh cervical levels (10 mm.), with the next greatest diameter at C_2 and C_8 (9 mm.). No lumbar (L_1; 7 mm.) swelling is present which is greater than the lateral diameter of L_1 (7 mm.). This situation may be partly accounted for by the fact that the second and third lumbar nerves originate from that part of the cord which lies at L_1. Again the largest nerves leaving the spinal cord in the cervical region are not only C_6 and C_7 but also C_2. Not knowing the structure of the spinal cord of any other primate than man the writer is at a loss to account for the size of the second cervical nerve.

The least lateral diameter in the thoracic region is found at T_8 (4 mm.). Below T_8 the breadth of the cord widens from 5 mm. (T_9) to 6 mm. (T_{10}–T_{12}). This situation may be correlated with the finding that marked sloping of the spinal nerves begins at T_{10}, so that the first lumbar nerve leaves the cord about 2 mm. below the twelfth thoracic level, and the roots of both L_2 and L_3 emerge from the cord at the height of the first lumbar vertebra. L_2 (7 mm.), which has as great a breadth as L_1, gives rise to L_4; and between L_2 and L_3 the spinal nerves of L_5 to S_2 emerge. S_3 arises just cephalad to L_4, and Ca_1, just caudad to L_4. The fine caudal nerves, 2 and 3, emerge between L_4 and L_5, so that the spinal cord terminates anterior to L_5, rather than at L_1 as in man.

The largest nerve trunk leaving the lumbar region is L_6; indeed the size of the lumbar nerves grow progressively larger, passing caudalward, although those of L_2 and L_3 are appreciably smaller than L_4. Consequently one would expect the diameter of the cord at L_2 to be greater than that of any other level in the lumbar region.

In comparative length the cervical region is one-seventh of the total length of the cord, the thoracic, a little more than one-third. The lumbar, the sacral and the caudal occupy together in the neighborhood of one-ninth, while the filum terminale takes up the more caudal third.

The writer trusts that this brief description of the external morphology of the brain of the rhesus macaque, together with the great interest in the physiology of its central nervous system, will prove a sufficient stimulus for someone to undertake a thorough investigation of the internal structure of the nervous system from a comparative point of view. Strangely, no brain of any primate other than that of man, has been studied intensively.

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CHAPTER XV

THE CRANIAL NERVES

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The cranial nerves of *Macaca mulatta*, i.e. the twelve pairs of nerves (fig. 100) which are connected with the brain, have been dissected from their points of origin or termination peripherally to their entrance into or exit from the brain. The descriptions begin with those special sensory pathways, the olfactory and optic, or first and second cranial nerves respectively, and continue with the other cranial nerves in consecutive order from the third to the twelfth. The illustrations of necessity do not follow this procedure, but represent the stages of dissections at which the courses of the nerves may be demonstrated to advantage. The gross appearances of the nerves have served chiefly for the relationships here described but, in a few instances, microscopic sections have aided in clarifying questions of structure. Chapter XIV with its illustrations should be consulted in connection with the present chapter.

I. THE OLFACTORY NERVES

(Fig. 101)

The olfactory nerves, which arise as fibers from sensory cells in the olfactory mucous membrane of the nose, are found medially in the upper part of the nasal septum and laterally over the superior surface of the nasal wall. These medial and lateral groups of filaments form plexuses in the connective tissue where, by careful removal of the surface of the mucosa, they may be demonstrated. A number of filaments arising from the plexuses at the roof of the nasal cavity pass through foramina in the cribriform plate and then through the meninges to end in the inferior surface of the olfactory bulb.

II. OPTIC NERVE

(Fig. 102)

The optic nerve is a large rounded nerve which carries fibers from multipolar ganglion cells in the retina of the eye to the thalamus and midbrain. The nerve passes obliquely upwards and backwards from the back of the eyeball somewhat medial to the center, and pursues a slightly wavy course through the orbit. It leaves the orbit through the optic foramen to join the anterolateral angle of the optic chiasma.

III. OCULOMOTOR NERVE

(Fig. 102)

The oculomotor nerve emerges from the oculomotor sulcus medial to the cerebral peduncle of the mesencephalon. It innervates the m. levator palpebrae superioris and all of the extrinsic eye muscles except the superior oblique and the lateral rectus muscles. Within the cranium the nerve runs forwards and lateralwards for a short distance to pierce the dura and continues in the lateral wall of the cavernous sinus. It enters the orbit through the superior orbital fissure, after which it passes through the annulus tendineus communis, and divides into a superior division and an inferior division separated from one another by the nasociliary nerve. The *superior division*, the uppermost in position and the smaller of the two, can be traced medianwards over the optic

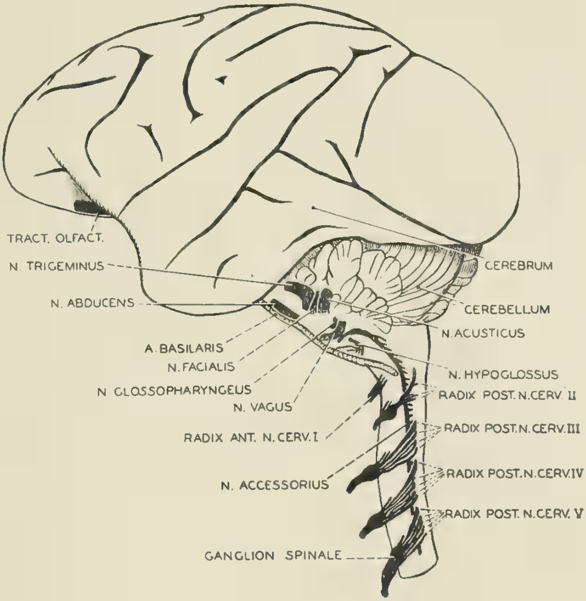

FIG. 100. Brain and part of the cervical spinal cord from the left side, to show the origins of some of the cranial nerves.

nerve to the ocular surfaces of the superior rectus and levator palpebrae muscles where it breaks up into a number of small filaments for their supply. The *inferior division*, situated below the nasociliary nerve and the larger of the two, divides near its origin into three branches. One short branch passes beneath the optic nerve and soon breaks up into a number of filaments which enter the ocular surface of the medial

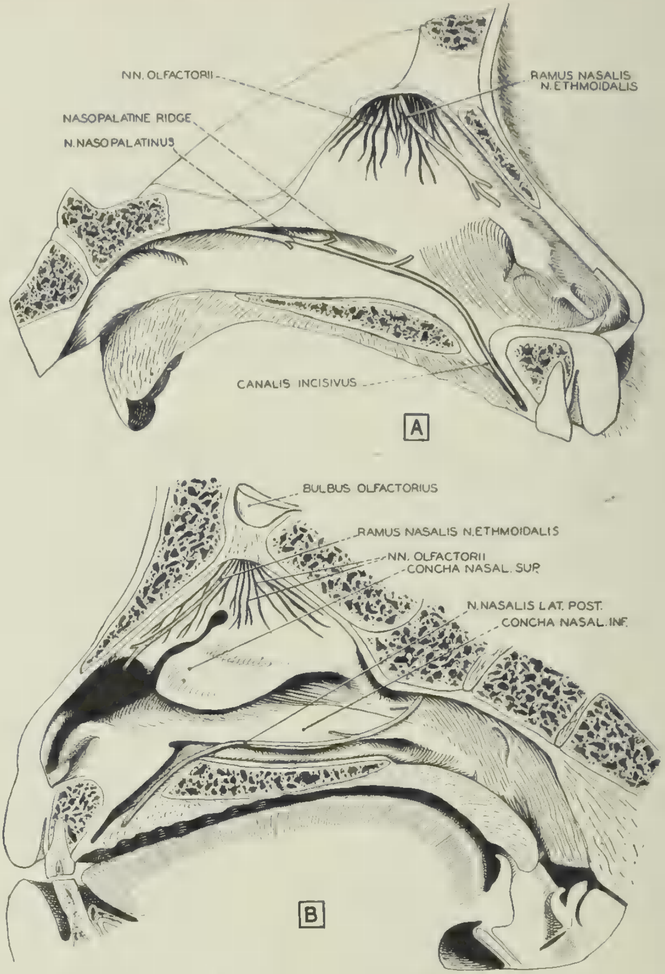

FIG. 101. A, nerves of the right median nasal wall. B, nerves of the right lateral nasal wall.

rectus muscle. The second branch breaks up into filaments which enter the ocular surface of the inferior rectus muscle. The third branch is prolonged forwards between the lateral and inferior recti muscles to end in the posterior border of the inferior oblique muscle close to its insertion. A short but broad attachment exists between the ciliary ganglion and the inferior oblique branch immediately beyond the origin of the latter.

IV. TROCHLEAR NERVE

(Fig. 102)

The trochlear nerve is small. It emerges from the anterior medullary velum close to the inferior colliculus and supplies the superior oblique muscle of the eye. It crosses the brachium conjunctivum, winds downwards and forwards about the cerebral peduncle, and then enters the dura. Passing forwards, it lies in the lateral wall of the cavernous sinus beneath the oculomotor nerve, which it crosses, and enters the orbit through the superior orbital fissure, and then medial to the frontal nerve it passes over the origin of the m. levator palpebrae superioris. It finally breaks up into a number of small filaments which enter the orbital surface of the superior oblique muscle near its origin.

V. TRIGEMINAL NERVE

(Figs. 103–106)

The trigeminal nerve, one of the larger cranial nerves, functionally is a mixed nerve. Sensory fibers from the head and face have their origin in the semilunar ganglion cells whose central processes enter the brain stem through the lower side of the pons. Motor fibers emerge through the pons and innervate the muscles of mastication. The motor root is situated medial to the sensory root. The semilunar ganglion is a large triangular ganglion on the sensory root of the nerve. From its base, which is directed lateralwards and forwards, three large nerves arise, viz., the ophthalmic, the maxillary and the mandibular. The ophthalmic and the maxillary nerves are sensory. The mandibular nerve is joined by the motor root and is, therefore, composed of both sensory and motor fibers.

The *ophthalmic* or first division of the trigeminal nerve, the smallest of the three branches, comes from the upper part of the semilunar ganglion. It passes through the wall of the cavernous sinus and enters the orbit through the superior orbital fissure. Just before entering the orbit, the nerve divides into three branches: the nasociliary, the frontal and the lacrimal nerves. The lacrimal and frontal nerves are large and appear as a bifurcation of the ophthalmic nerve. The nasociliary nerve is small and arises somewhat medial to and back of the frontal nerve. The frontal nerve, slightly smaller than the lacrimal nerve, in the orbit proceeds forward over the surface of the m. levator palpebrae superioris and in front of the orbit divides into a number of small filaments lateral to the trochlea of the superior oblique muscle. These form the supratrochlear nerves which supply the skin of the forehead, the upper eyelid, the conjunctiva and the frontal region of the head. The lacrimal nerve passes forwards in the orbit along the upper border of the lateral rectus muscle. It gives off branches to the lacrimal gland and large branches continue into the upper eyelid to supply the skin and conjunctiva. The latter branches form a supraorbital nerve. The nasociliary nerve passes forwards in the orbit between the superior and inferior divisions of the oculomotor nerve, crosses the optic nerve, and then turning median-

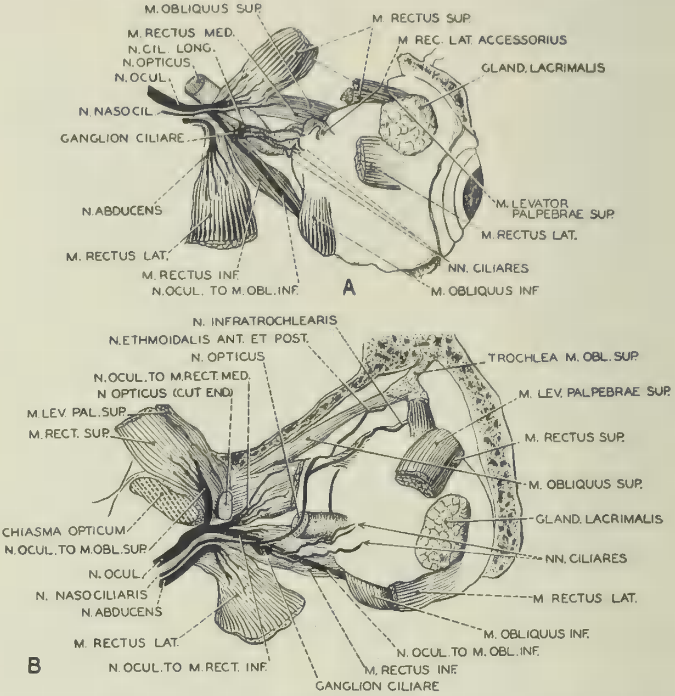

FIG. 102. A, the nerves of the right orbit from the right side. B, deeper nerves of the right orbit from above; a part of the optic nerve has been removed.

wards it divides near the superior surface of the medial rectus muscle into the infratrochlear nerve and the ethmoidal nerve. The infratrochlear nerve passes forwards beneath the trochlea of the superior oblique muscle and ends in the skin of the eyelids and the root of the nose. The ethmoidal nerve passes lateralwards and gives off branches to the internal and external surfaces of the nose. Before the nasociliary nerve crosses the optic nerve it gives off a branch, the long ciliary nerve, which connects with the ciliary ganglion and continues forwards to the eye.

The *maxillary*, or second division of the trigeminal nerve, arises from the middle of the semilunar ganglion. It leaves the skull through the foramen rotundum, crosses the pterygopalatine fossa, passes lateralwards on the back of the maxilla, and enters the orbit through the inferior orbital fissure. In the orbit, this nerve divides into a number of branches, the infraorbital nerves, which pass along the floor of the orbit and emerge onto the surface of the face through the infraorbital foramina, where they divide profusely into filaments supplying the side of the nose, the lower eyelid and the upper lip. These infraorbital endings join terminal branches of the facial nerve and form a complex plexus. The sphenopalatine nerves are small nerves which leave the submaxillary nerve in the pterygopalatine fossa and join the sphenopalatine ganglion posteriorly. The nerve of the pterygoid canal also joins the ganglion posteriorly. The superior alveolar nerves, carrying fibers to the upper jaw, consist posteriorly of several branches arising from the maxillary nerve in front of the sphenopalatine nerves and anteriorly of branches arising from the infraorbital nerves. The branches which innervate the teeth are small and only with difficulty can they be followed in the cancellous bony tissue of the maxilla.

The *mandibular*, or third division of the trigeminal nerve, is made up of sensory components arising from the inferior angle of the semilunar ganglion and the motor root. It emerges from the skull through the foramen ovale. The *nerve to the internal pterygoid muscle*, which arises from the posteromedial side of the mandibular nerve, passes forwards to the deep part of the upper end of the muscle. Immediately below, the mandibular nerve is divided into anterior and posterior parts; the anterior part consists chiefly of the motor fibers while the posterior part contains mainly the sensory fibers. The branches of the anterior part are the masseteric, the deep temporal, the external pterygoid and the buccinator nerves. The masseteric nerve passes lateralwards in front of the temporomandibular articulation and crosses the mandibular notch to the deep surface of the masseter muscle. The *deep temporal nerves* have a common root with the masseteric nerve. They pass lateralwards and forwards above the external pterygoid muscle and then turn upwards to the temporal muscle, where branches are given off to the deeper parts of the muscle. The anterior part of the mandibular nerve continues forwards between the two heads of the external pterygoid muscle, and, along its course, gives off several small *external pterygoid nerves*, while the main branch continues forward as the *buccinator nerve* which terminates in the walls of the cheek and mouth. The first branch of the posterior division of the mandibular nerve is the *auriculotemporal nerve*, which arises by several roots from the posterolateral surface of the nerve trunk. It runs obliquely backwards to the medial side of the neck of the mandible where, between the condyle of the mandible and the auricle of the ear, it turns upwards in close relation to the anteromedian surface of the parotid gland. It crosses the zygoma and then breaks up into superficial temporal branches. The branches of the nerve include filaments to the posterior part of the mandibular joint, to the interior of the external auditory meatus, to the anterior part of the auricle and to the parotid gland. The inferior alveolar nerve, a large branch, is

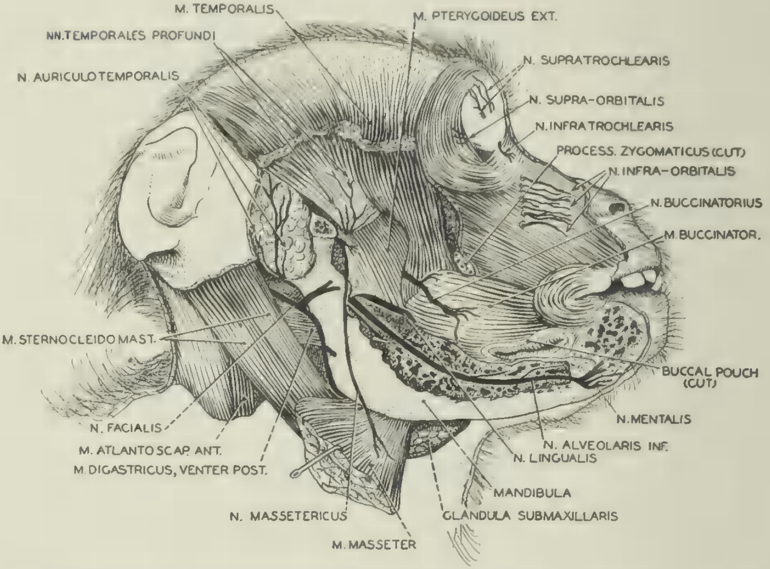

FIG. 103. Dissection of the right side of the head to show the branches of the mandibular nerve. The masseter muscle has been turned lateralwards, the mandibular canal opened, and the zygomatic arch and the coronoid process of the mandible removed.

given off from the mandibular nerve posterolateral to the lingual nerve, along the side of which it lies for some distance downwards. The inferior alveolar nerve arises near the lower border of the external pterygoid muscle, enters the mandibular foramen and passes forwards in the mandibular canal beneath the molar and premolar teeth, to which it supplies dental branches. At the mental foramen, the mandibular nerve divides into two terminal branches: the incisive nerve and the mental nerve. The *incisive nerve* continues within the bone to supply the incisor and canine teeth. The *mental nerve* emerges from the mental foramen and divides into small branches supplying the skin of the lower lip and the chin. The *lingual nerve*, which branches from the posterior part of the mandibular nerve at the same level as the inferior alveolar nerve, descends to the lower border of the external pterygoid muscle, and passes downwards and forwards between the internal pterygoid muscle and the mandible to the submaxillary region, where small rami are given off to the submaxillary ganglion and the ganglion cells supplying the sublingual gland. It then passes obliquely to the side of the tongue and finally terminates in the tongue. The chorda tympani, a branch of the facial nerve, joins the lingual nerve a short distance below its origin. The *mylohyoid nerve* arises from the posterior edge of the mandibular nerve just a little below the auriculotemporal nerve. It

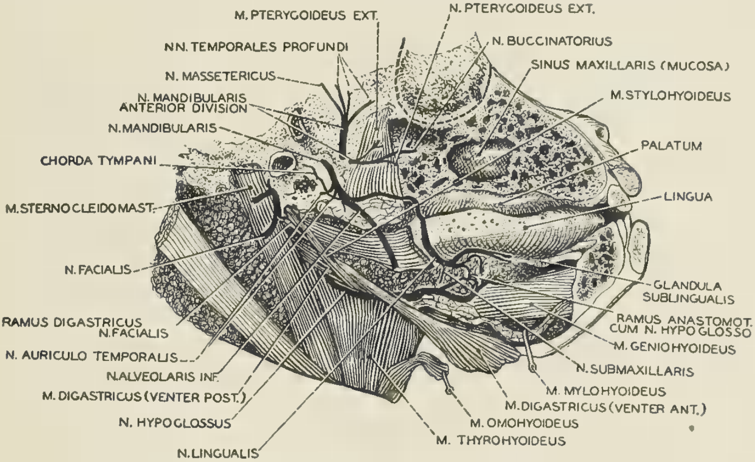

FIG. 104. Dissection of the right side of the head to show the branches of the facial nerve going to the stylohyoid and the digastric muscles; branches of the mandibular nerve are also to be seen. Much of the right half of the maxilla and most of the mandible have been removed.

follows the inferior alveolar nerve as far as the mandibular foramen, then passes forwards on the medial surface of the mandible. Its terminal branches supply the mylohyoid muscle and the anterior belly of the digastric muscle.

The parts of the cranial autonomic system which have intimate anatomical relationships with the branches of the fifth cranial nerve, but which have their functional connections through branches of the third, seventh and ninth cranial nerves, are described in chapter XVII.

VI. ABDUCENT NERVE

(Fig. 102)

The abducent nerve emerges from the anterior median surface of the medulla at the inferior border of the pons and innervates the lateral rectus muscle of the eye. This nerve, although small, is much flattened near its origin. It passes forwards for a short distance, penetrates the dura below and medial to the fifth nerve, traverses the cavernous sinus and enters the orbit through the superior orbital fissure. It reaches the ocular surface of the lateral rectus muscle where it breaks up into a number of filaments near the origin of the muscle.

VII. FACIAL NERVE

(Figs. 103–105) (See also chapter VIII, figs. 53–55)

The facial nerve, which innervates the superficial facial musculature, certain deep muscles, and also provides some sensory fibers to the head, emerges from the brain at the lower border of the pons, just in front of the acoustic nerve. Its two roots, motor and sensory, are closely applied to each other shortly after their appearance and in the internal auditory meatus they unite to form a single trunk. Situated above the acoustic nerve, the facial nerve, in its course from the brain and in the internal auditory meatus, passes lateralwards and upwards. As the nerve turns backwards and lateralwards into the facial canal it shows an ovoid swelling, the geniculate ganglion, from which the sensory fibers originate. Here the first branches of the facial nerve are given off. Situated in grooves in the petrous bone, they can be exposed only after the semilunar ganglion which lies over them has been turned forwards and outwards. Of these branches, the petrosal nerves, the greater superficial petrosal nerve especially should be considered. It arises from the geniculate ganglion, passes forwards and unites with the deep petrosal nerve to form the *nerve of the pterygoid canal.* In the facial canal, near its lower end, the facial nerve gives off a small branch to the stapedius muscle. A little beyond this it gives off a large branch, the *chorda tympani*, which enters the tympanic cavity through a small aperture close to the posterior margin of the tympanic membrane, passes forwards over the surface of the tympanic membrane and the handle of the malleus, and, at the anterior limit of the tympanic cavity, leaves the skull. A short distance below, passing downwards and forwards, it joins the posterior border of the lingual nerve and forms the chorda-lingual trunk through which motor fibers of the facial nerve are distributed to the submaxillary ganglion and sensory (taste) fibers chiefly to the anterior part of the tongue. After leaving the stylomastoid foramen, the facial nerve gives off the posterior auricular branch. A short distance below, the next branch to appear is a small nerve, the digastric, which divides into two branches, one of which supplies the posterior belly of the digastric muscle, and the other, the stylohyoid muscle. The remaining branches of the facial nerve, including the posterior auricular branch, are described in chapter VIII.

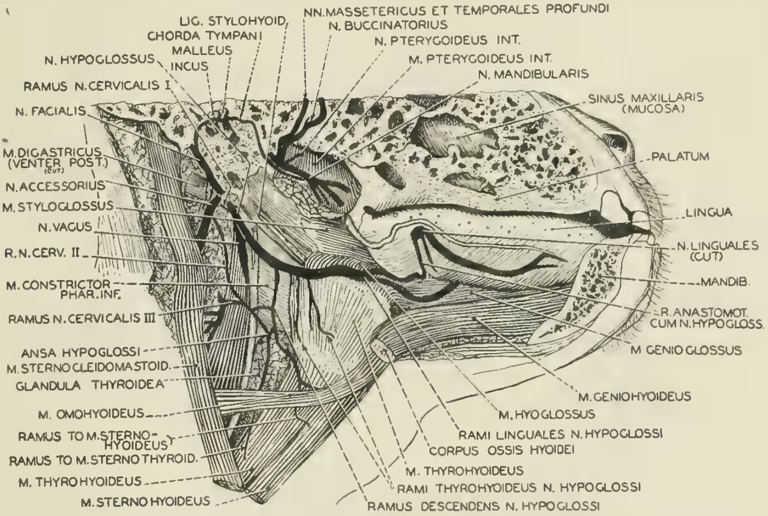

FIG. 105. Dissection to show the hypoglossal nerve, and its branches on the right side. A portion of the chorda tympani is shown.

VIII. ACOUSTIC NERVE

(Fig. 100)

The acoustic nerve, carrying fibers from the ear to the medulla, consists of two divisions: a cochlear division whose fibers enter the medulla posteriorly and a vestibular division whose fibers enter anteriorly. A number of filaments coming as central fibers from the spiral ganglion located in the modiolus of the cochlea form the *cochlear* division. Neurons in the vestibular ganglion whose peripheral processes supply the utricle, the superior and lateral semicircular canals, the saccule, and the inferior semicircular canal send fibers centralwards which compose the *vestibular* division. In the internal auditory meatus the two divisions unite in a large common trunk which is associated with the facial nerve, the acoustic nerve being the lower of the two. Emerging from the internal auditory meatus, the acoustic nerve is still below the facial nerve and posterior to it. It passes medianwards to enter the medulla at the lower border of the pons just back of the facial nerve.

IX. GLOSSOPHARYNGEAL NERVE

(Fig. 106)

The glossopharyngeal nerve is a mixed nerve supplying the tongue and pharynx. It arises from the posterolateral side of the medulla by a number of rootlets in series with the vagus roots below. The nerve passes lateralwards and lying in a tube of dura above the vagus nerve leaves the cranial cavity through the jugular foramen. In the jugular foramen ganglionated areas of the nerve occur as slightly ovoid enlargements in which cells of the superior and petrous ganglia can be demonstrated microscopically. The *tympanic* nerve, which runs as a minute branch from the petrous ganglion to the tympanic cavity, can scarcely be followed. This nerve carries visceral efferent fibers destined for the otic ganglion. Outside the skull the glossopharyngeal nerve is found in intimate association with the vagus, accessory and hypoglossal nerves as it passes downwards and forwards. In the neck it divides into two large branches: One posterior and the other anterior. The posterior branch descends beside the internal carotid artery and in its upper course gives off pharyngeal branches which contribute to the formation of the pharyngeal plexus together with vagus fibers. The termination of the descending branch is at the origin of the internal carotid artery and here it ends in the arterial wall as the *nerve to the carotid sinus*. The anterior branch, passing obliquely forwards, also contributes some small pharyngeal branches, and as it crosses the stylopharyngeal muscle gives off a branch to it. Curving anteriorly, the nerve gives off filaments to the mucosa in the region of the palatine tonsil and the soft palate, but the main branch enters the tongue as the lingual branch, which supplies the glands of the posterior half of the tongue and the mucous membrane, especially the taste buds.

X. VAGUS NERVE

(Figs. 105, 106, 107)

The vagus nerve is a mixed nerve which supplies many of the visceral organs with both sensory and motor fibers and innervates the striated musculature of palate, pharynx and larynx. The rootlets of the vagus nerve arise from the posterolateral portion of the medulla between the roots of the glossopharyngeal and accessory nerves. Passing lateralwards the vagus nerve leaves the cranial cavity through the jugular foramen. In its upper part it lies in front of the hypoglossal and accessory nerves and behind the glossopharyngeal nerve. In the jugular foramen

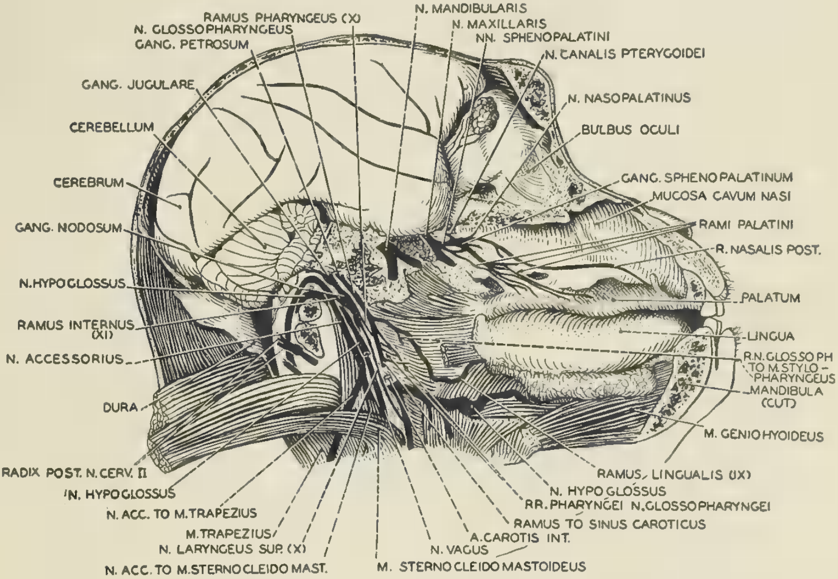

FIG. 106. Dissection to show especially (1) the nerves of the upper pharynx and their relation to the brain; (2) the sphenopalatine ganglion and its nerves. The right side of the brain is shown; the right orbit is opened; and the outer side of the right lateral nasal mucous membrane may also be seen.

it shows an ovoid enlargement, the jugular ganglion, and just outside the skull there is a second enlargement, the nodose ganglion. The ganglia are the sources for three vagus branches. The *auricular* nerve, arising from the vagus at the level of the jugular ganglion, traverses the temporal bone to be distributed to the skin of the back of the auricle and to the posterior part of the external auditory meatus. The *pharyngeal* branch comes from the upper part of the nodose ganglion, proceeds obliquely downwards and forwards, and in the vicinity of the pharyngeal branches of the glossopharyngeal nerve breaks up into fine filaments which form a part of the *pharyngeal plexus.* The *superior laryngeal* nerve is a larger nerve arising from the nodose ganglion lower down. Passing forwards beneath the internal carotid artery it shortly divides into branches which supply superior and inferior parts of the larynx. In the neck the vagus nerve has a vertical course downwards from the nodose ganglion. At first it is located alongside of the internal carotid artery and lower down it has a similar position beside the common carotid artery. When the vagus nerve enters the thorax on the right side it crosses the subclavian artery. Just as it passes over the subclavian artery, the vagus gives off the *right recurrent* nerve which curves about the subclavian artery and ascends obliquely beneath the common carotid artery along the side of the trachea. The recurrent nerve continues upwards between the trachea and esophagus and terminates in the larynx. Branches from the recurrent nerve are given off to the cardiac plexus, the esophagus, the trachea, the pharynx, and the larynx. The *cardiac* branches of the vagus have a low origin. The first cardiac nerve on the right side is given off near the origin of the recurrent nerve. This branch passes obliquely downwards and enters the cardiac plexus. Another cardiac nerve arises from the vagus a little below the origin of the recurrent nerve, and also passes obliquely towards the heart to reach the cardiac plexus. In the thorax the vagus nerve of the right side descends along the side of the trachea to the back of the root of the lungs. *Bronchial* nerves are distributed to the anterior surface of the root of the lungs and form a part of the anterior pulmonary plexus. Their fibers also spread over the base of the lungs posteriorly to form a part of the posterior pulmonary plexus. *Esophageal* branches are given off from the vagus both above and below the bronchial nerves. The branches to the lower esophagus are prominent and more numerous. They contribute fibers to the esophageal plexus. Below the lower part of the pulmonary plexus, the right vagus shows anastomosing branches which unite shortly to form a single cord. A communicating branch from the left vagus unites with the right below this anastomosis. In the abdomen, the right vagus nerves give rise to branches which form a network of nerve fibers, the *posterior gastric plexus*, situated over the posterior and inferior parts of the stomach. The *coeliac* branches which form the terminals of the vagus on the right side are distributed to the pancreas, spleen, suprarenal bodies and intestine. The upper parts of the left vagus are similar to those of the right vagus. The left vagus nerve enters the thorax between the left common carotid artery and the subclavian artery. Above the arch of the aorta, several cardiac branches are given off. The vagus then crosses the arch of the aorta where it gives off the *left recurrent* nerve, which curves about the arch of the aorta and ascends obliquely in the same manner as the right recurrent nerve. The left vagus nerve in the thorax descends behind the root of the left lung, from which numerous branches are given off to the pulmonary plexus. Numerous esophageal branches also are prominent on this side in the region of the lungs. Below the pulmonary plexus, the left vagus has connections with the right. The left vagus then continues to the stomach where branches are given off to the superior and anterior surfaces, forming an *anterior gastric plexus*.

XI. ACCESSORY NERVE

(Figs. 105, 106)

The accessory nerve, innervating certain muscles of the neck and back and also contributing fibers to muscles receiving branches of the vagus nerve, arises from both medulla and spinal cord. The cranial or *internal portion* of the accessory nerve arises by rootlets from the posterolateral side of the medulla slightly below the origin of the vagus nerve. The spinal or *external portion* of the accessory nerve consists of a slowly tapering trunk lying along the side of the spinal cord beneath the posterior spinal nerve roots as far as the fourth, fifth, or sixth cervical segment. It arises by rootlets which emerge through the lateral funiculus of the spinal cord and enters the cranium through the foramen magnum. Near the cranial accessory nerve and the vagus, it becomes enclosed with these nerves in a common dural sheath and leaves the cranium through the jugular foramen. The cranial fibers are incorporated with the vagus nerve at the nodose ganglion and are distributed chiefly through the pharyngeal and superior laryngeal branches of the vagus nerve and to some extent also through the recurrent and cardiac branches. Through the pharyngeal branch especially the accessory nerve fibers go to the

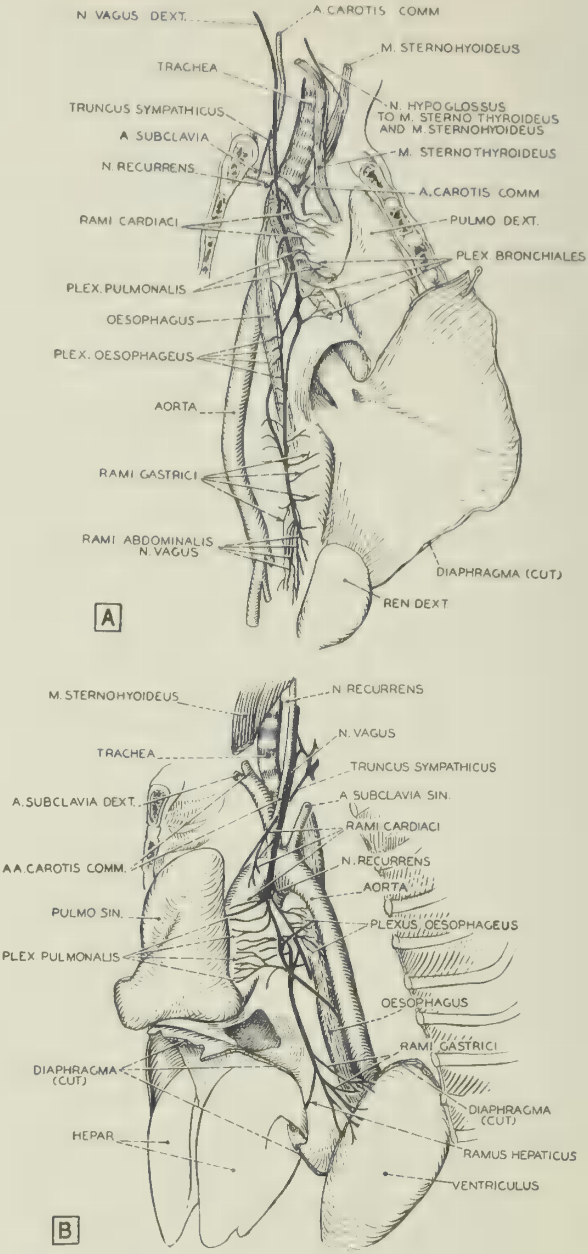

Fig. 107. A, dissection of the right vagus nerve. Organs in thorax and abdomen have been turned to the left. B, dissection of the left vagus nerve. Organs have been turned to the right.

levator veli palatini muscle. The spinal portion of the accessory nerve below the skull is found outside and posterior to the hypoglossal nerve. When medial to and below the digastric muscle, the accessory nerve passes through the sternocleidomastoid muscle complex, to which it gives off branches, and continues downwards to the lower inner surface of the trapezius muscle, where it breaks up into branches supplying this muscle. At the level where the branches to the sternocleidomastoid muscle are given off, communicating branches of the second and third cervical nerves join the accessory nerve. Tanaka (1932) has studied the cranial nerves involved and the various connections made between cranial nerves and the accessory nerve in the formation of an accessorocervical plexus. He found that communicating branches in some cases were derived from the second, third and fourth cervical nerves, from the third and fourth in other cases; and also from the second and third cervical nerves. (Also cf. chapter XVI.)

XII. HYPOGLOSSAL NERVE

(Figs. 104, 105, 106, 107)

The hypoglossal nerve conveys motor fibers from the medulla to the tongue muscles and to many of the muscles attached to the hyoid bone. The rootlets of this nerve are found on the anterolateral portion of the medulla at a level medial to the roots of the accessory nerve. The nerve pierces the dura and leaves the cranium through the hypoglossal canal. Outside of the skull it at first lies beneath the accessory nerve, then curves about the nodose ganglion of the vagus nerve and comes to lie beside the internal carotid artery. At the level of the digastric muscle it curves forwards and passes towards the tongue, crossing the internal and external carotid arteries, and passing medially to the digastric, the stylohyoid, and the mylohyoid muscles. Above the point where it starts to turn forwards, it is joined by a communicating branch from the first cervical nerve. The *descending branch* of the hypoglossal nerve is given off just after the nerve curves forwards. A short distance in front of the descending branch, two branches are given off to the thyrohyoid muscle. The remainder of the nerve anterior to the thyrohyoid branches innervates the tongue muscles, including the styloglossus, the hyoglossus, the genioglossus, the geniohyoideus and the intrinsic musculature. A branch communicating with the lingual nerve is given off from the hypoglossal nerve near the anterior border of the hyoglossus muscle.

Communicating branches of the second and third cervical nerves unite with the descending branch of the nerve to form a loop, the *ansa hypo-*

glossi, from which branches to the infrahyoid muscles arise. In some instances a branch proceeds almost directly downwards to supply the lower portion of the omohyoid muscle. A large branch arising at the level of the ansa hypoglossi passes to the upper parts of the sternohyoid muscle and filaments also supply the upper part of the omohyoid muscle. A little lower, another branch which crosses the inferior tip of the thyroid gland supplies the upper sternothyroid muscle. The lowest parts of the sternohyoid and sternothyroid muscles are reached by a descending branch which follows along the lateral margin of the sternohyoid muscle and gives off filaments to each muscle near its origin. It is probable that there are variations in the connections of the cervical nerves with the hypoglossal nerve. The hypoglossocervical plexus figured by Tanaka (1932) resembles the description given here. (See also chapter XVI.)

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Chapter XVI

THE SPINAL NERVES

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The peripheral spinal nervous system in its broader sense is composed of somatic, and visceral or autonomic (sympathetic and parasympathetic) divisions. The former is made up of sensory or receptor (afferent) fibers, conducting sensory impulses from the periphery to the central nervous system, and of so-called motor or effector (efferent) fibers from the central nervous system to the muscles. Peripheral nerves as encountered during dissection are either considered as sensory branches, although they contain some efferent autonomic fibers, or muscle (erroneously termed motor) nerves, which in addition to motor fibers contain sensory (as well as autonomic) fibers to the muscles.

It should be realized that this description of the peripheral nerves of the rhesus macaque is based upon the dissection of a limited number of specimens, and that variations will constantly be encountered.

In the rhesus macaque there are 34 pairs of spinal nerves, comprising 8 cervicals, 12 thoracics, 7 lumbars, 3 sacrals, and 4 caudals (Hines, in chapter XIV of this book, describes only 33 pairs). Each nerve emerges from the cord by two series of root filaments, a ventral (or anterior) derived from the ventral part of the cord, with cell bodies in the ventral gray column, and a dorsal (or posterior) from the dorsal portion of the cord, with cell bodies in the dorsal root ganglion. The ventral root is composed of somatic and visceral motor fibers, and the dorsal of somatic and probably visceral sensory elements. The two roots pass to the intervertebral foramen, where there is a dilation of the dorsal root for the accommodation of the spinal ganglion. The roots then fuse, but immediately separate once more to form the ventral and dorsal rami, fundamentally characteristic of all spinal nerves. Just before this division takes place there is given off a fine meningeal or recurrent branch, and just afterward, one (in the cervical and lower lumbar regions) or two (in the thorax) small rami communicantes to the sympathetic trunk.

The first cervical nerve is an exception in that the dorsal root and ganglion are apparently normally absent in the rhesus monkey (see figs.

95, 98, 99, 100). This absence was bilateral in three specimens examined by the present writers. Sherrington (1898) also noted the absence of the dorsal root of the first cervical nerve in the rhesus monkey as well as in the closely related bonnet monkey. According to him, both dorsal root and ganglion are usually present in the chimpanzee, but not in the orang-utan and cynomorphic apes; furthermore, root and ganglion are apparently regularly present in the common laboratory animals (dog, cat, rabbit, guinea-pig). It is well known that the dorsal root may be absent in man.

The dorsal ramus of each spinal nerve is short, dividing into lateral and medial divisions to supply the musculature and skin of the back. In the thorax each ventral ramus passes laterally and then ventrally in an intercostal space, where the nerve exhibits ventral and lateral divisions, supplying the skin and musculature of the thorax and abdomen. In the cervical and lumbosacral regions the ventral rami of the spinal nerves largely go to make up, respectively, the cervicobrachial and lumbosacral plexuses. There are ventral and dorsal cords of the parts of these plexuses supplying the limbs, analogous to the ventral and lateral divisions of the intercostal nerves. It is important that this basic subdivision be constantly kept in mind, for their branches supply respectively the ventral and dorsal, or flexor and extensor, musculature of the limbs, and a thorough understanding of myology cannot be gained without a proper appreciation of this detail.

In the following description no account has been taken of articular innervation.

Rami Ventrales

These will be considered first. Those of the cervical and first two thoracic nerves anatomose in a complicated manner to form the cervicobrachial plexus, described in two parts.

PLEXUS CERVICALIS

(Fig. 108)

The rami ventrales of the four upper cervical nerves enter into the formation of this plexus, although the direct contribution of C1 is very small or apparently even lacking. The roots of the nerves first emerge from between the m. longus capitis and mm. scaleni, and the more superficial branches of the plexus may be looked for along the posterior border of the m. cleido-occipitalis. Division is logically made into superficial cutaneous and muscular branches.

A. Rami cutanei

1. *N. occipitalis minor*, from C2 or C3, or both, is the more dorsal of the ascending divisions, sending one or two branches to the skin behind the ear.

2. *N. auricularis magnus*, likewise from C2 or C3, or both, is the cutaneous division distributed to the immediate base of the ear and supplying the skin just posterior thereto.

3. *N. cutaneus colli.* By juncture of branches from C3 and C4 there arises a nerve which pierces the m. atlantoscapularis anterior. This usually splits into two divisions, one of which anastomoses with the branch of the n. accessorius going to the m. trapezius, while the other becomes the n. cutaneus colli, supplying the skin over the front of the neck.

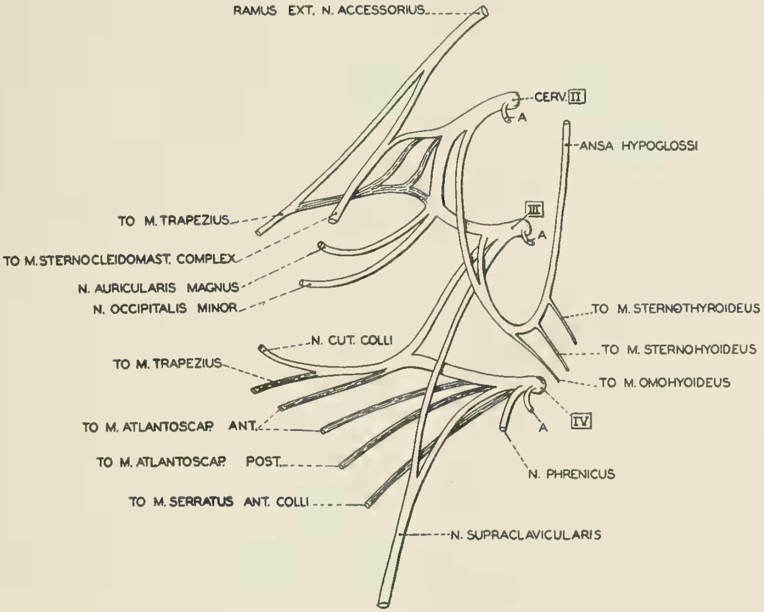

FIG. 108. Dissection of a right cervical plexus. A, short branches to the neck muscles.

4. *N. supraclavicularis* is the descending part of the cutaneous group, distributed to the skin over and just below the clavicle, and over the shoulder. At first it is single, arising from C3 and C4, later breaking up into divisions corresponding to the anterior, medial and posterior branches in man.

B. Rami musculares

1. The direct, cervical contribution to the *ansa hypoglossi* (formed by union of the ramus descendens n. hypoglossi with upper nn. cervicales) comes from C2 and C3. This passes just deep to the m. omohyoideus and superficial to the internal jugular vein; at about the level of the third or fourth cervical vertebrae it curves upward to join the ramus descendens n. hypoglossi. From the loop thus formed are given off branches to the *mm. omohyoideus*, *sternohyoideus*, and *sternothyroideus.* At times there may be an accessory connection between the two rami of the ansa. (Also see chapter XV.)

2. A branch from C2 to the *mm. sternomastoideus*, *cleidomastoideus*, and *cleido-occipitalis*, this usually first anastomosing with the n. accessorius.

3. Branches to the *m. trapezius* as follows: (1) an upper branch derived from C2 and C3, passing superficial to the m. atlantoscapularis anterior and anastomosing with the n. accessorius before the latter disappears beneath the border of the m. trapezius; (2) a lower branch to the m. trapezius diverging from the stem of the n. cutaneus colli, and hence appearing to come from C3 and C4. It pierces the m. atlantoscapularis anterior and anastomoses with the n. accessorius well under cover of the m. trapezius; (3) a third branch may arise from C4, at first associated with the branch to the m. atlantoscapularis posterior, reaching the m. trapezius by passing around the border of the former muscle.

4. Two, or even three, branches to the *m. atlantoscapularis anterior*, one from C4 and the other apparently from both C3 and C4.

5. A branch from C4 to the *m. atlantoscapularis posterior.*

6. One or two branches from the root of C4 to the cervical part of the *m. serratus anterior.*

7. A contribution from C4 to the *n. phrenicus*, which is derived from either this root alone or from both C4 and C5, and then passing deep to the rest of the plexus and downward to reach the *m. diaphragma.*

8. Extremely short branches from the roots of the cervical nerves to the *mm. rectus capitis anterior*, *rectus capitis lateralis*, *longus capitis*, *longus colli* and *scaleni* (and *intertransversarii?*).

In addition C1 communicates with C2 by a short anastomosis, and account should be taken of the course of the *ramus externus n. accessorius*, listed with the cranial nerves (See chapter XV). From the jugular foramen it passes down the neck and to the *m. trapezius* and the *sternocleidomastoid* complex.

PLEXUS BRACHIALIS

(Fig. 109)

The rami ventrales of the spinal nerves from the fifth cervical to the first thoracic inclusive, and a considerable portion of the second thoracic, compose the brachial plexus. Its roots appear from between the mm. scalenus brevis anterior and scalenus brevis posterior, and the interval between it and the cervical plexus is considerable, so that the two appear more segregated than in man. There is either no connection between them or else the hiatus is bridged by one root of the n. phrenicus. The plexus is formed in a progressive manner on an idealistic plan, some of the features of which may not always be readily apparent for the reason that anastomoses or divisions may occur more proximally or distally than suggested. Broadly stated, C5 and C6 unite, just distal to their exit from the intervertebral foramina, to form the so-called upper trunk of the plexus; C8 and T1 (together with the contribution from T2) anastomose to form the lower trunk; while C7 alone comprises the middle trunk (see fig. 109). Theoretically, below the trunks, there is redistribution of nerve components, by branching divisions (which may occur before the trunks are actually formed) and later anastomoses, to form the primary cords of the plexus, of which there are three. The dorsal (or posterior) cord is produced by the union of the dorsal elements of all three trunks, and thus contains elements of at least the five upper nerves (probably not T2) contributing to the formation of the plexus. The lateral cord is formed by the junction of the ventral (or anterior) divisions of the upper and middle trunks (C5, C6, C7); and the medial cord by the ventral division of the lower trunk (C8, T1, T2). The cords then break up into the secondary nerve branches.

The dorsal or posterior cord supplies the nerves to every extrinsic and intrinsic muscle of the shoulder region except the pectoral group of muscles (including m. subclavius), and to the extensor musculature of arm and fore arm. The lateral cord contains nerve elements supplying the flexors of the arm (n. musculocutaneus), a part of those to the pectoral region, and a part of the n. medianus to most of the flexors of the fore arm and hand, as well as cutaneous sensory branches to the fore arm. The medial cord contributes to a part of the pectoral innervation, the cutaneous nerves to the flexor surface of the appendage, all of the n. ulnaris and a part of the n. medianus, which together supply the flexor musculature of fore arm and hand. The nerves of the plexus will be grouped into short, deep, muscular branches (impractical to divide into dorsal and ventral elements), longer dorsal components, and ventral components.

A. Rami Musculares

Rami musculares short and deep, from the roots of the nerves forming the plexus, go to *mm. scaleni* and *longus colli.*

B. Nerves of the dorsal group (posterior cord)

1. *N. dorsalis scapulae*, from C5 only, emerges from its root usually not with the rest of the plexus but deep to the mm. scaleni breves. It divides into two branches, one of which innervates, in company with twigs from C4, the cervical portion of the *m. serratus anterior*, while the other, piercing this muscle sheet, is distributed to the *m. rhomboideus.*

2. *N. thoracalis longus* is consecutive with the last, the two together forming the so-called nn. thoracales posteriores. It arises from the four nerves C5 to C8, passes rearward deep to the mm. scaleni, over the lateral surface of the m. serratus anterior, and supplies the thoracic portion of the latter muscle sheet.

3. *N. suprascapularis*, from C5 and C6, is the upper one of the more apparent branches of the plexus. It passes directly to the suprascapular notch and thence beneath the *m. supraspinatus*, which it innervates (as well as the *m. intraspinatus*, when this is differentiated as a separate slip). The rest of the nerve passes over the great scapular notch to enter the substance of the *m. infraspinatus.*

4. *Nn. subscapulares* vary in number from two to as many as five branches distally adjacent to the n. suprascapularis and arising from C5 to C6. They pass directly to the medial belly of the *m. subscapularis.*

5. *N. teres major* is next in series, branching from the posterior cord of the plexus with the n. axillaris and twisting deep to the latter. It is derived from C5, C6, and probably C7, and passes directly to the *m. teres major.*

6. *N. thoracodorsalis* is derived either from both C7 and C8 or from the former alone. It passes beneath (dorsal to) the other long components of the plexus and to the upper part of the medial belly of the *m. latissimus dorsi.*

7. *N. axillaris* arises from C5, C6 and C7. It splits into two parts just before it disappears between the mm. coracobrachialis and teres major. Its course is then about the surgical neck of the humerus and between the m. triceps and *m. teres minor.* It supplies the latter muscle as well as the *m. deltoideus*, which covers it, and also gives rise to a num-

ber of cutaneous branches (n. cutaneus brachii lateralis) which emerge from under the posterior border of the m. deltoideus and innervate the surrounding skin.

8. *N. radialis.* Because of the position of the connections between C6 and C7 it is frequently difficult to be certain of the number of roots entering into the composition of this nerve. All five of the upper elements may be involved, as in man, but Sherrington's (1898) investigations suggest that only C6—T1 may be included. The radial nerve passes for some distance down the upper arm with the other appendicular nerves. With some of its muscular branches, it then passes spirally behind and to the lateral side of the humerus between the lateral and medial divisions of the m. triceps, and pierces the original part of the m. brachioradialis.

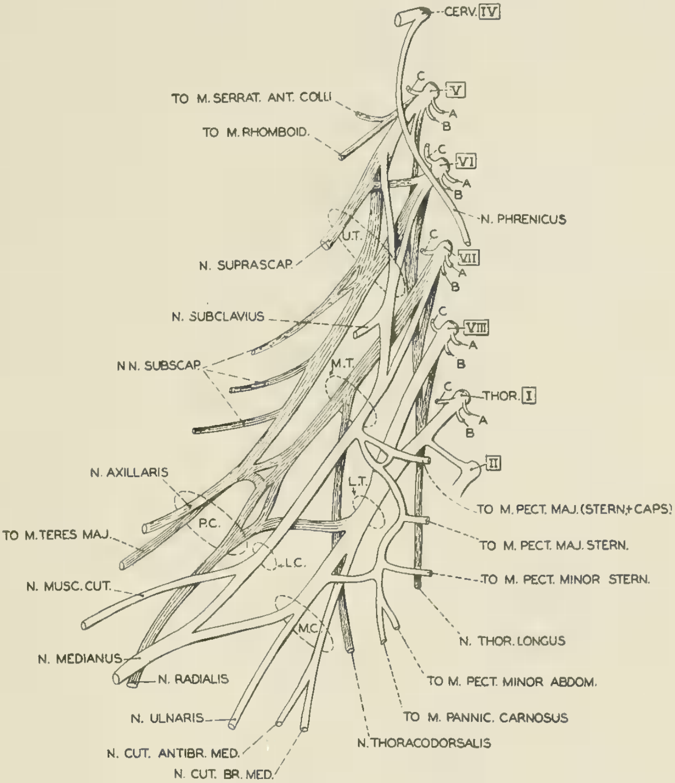

FIG. 109. Dissection of a right brachial plexus. A, branches to m. longus colli; B and C, branches to mm. scaleni.

Just above the elbow it therefore lies between the latter muscle and the m. brachialis, and here splits to form the superficial and deep branches. In its course it gives off the following branches:

(a) *Rami musculares* split off well up the arm, to supply the *mm. dorso-epitrochlearis*, the *triceps longus* by several high twigs, and lower in the arm the *triceps medialis* and *lateralis*. Between the latter divisions a long branch descends to the *m. anconeus lateralis.*

(b) *Nn. cutanei brachii posteriores* are given off from the radial nerve in its upper part and are distributed to the skin about the posterior margin of the axilla.

(c) *N. cutaneus antibrachii dorsalis* emerges upon the lateral side of the upper arm from between the mm. triceps lateralis and brachialis, and is distributed to the skin over the lateral part of the fore arm.

(d) *Ramus superficialis* is cutaneous. It separates above the elbow and passes between the mm. brachioradialis and supinator. Just above the wrist it emerges subcutaneously from between the mm. brachioradialis and extensor carpi radialis longus and there divides into three main branches. The middle of these continues toward digit III, the lateral (ulnarward) toward digit IV, and the medial toward the thumb.

(e) *Ramus profundus* is a muscular branch. From above the elbow it passes between the mm. extensor carpi radialis longus and brachialis to the medial border of the m. supinator, which it pierces. It extends along the fore arm deep to the extensor carpi radialis layer, and in its course gives off rami musculares to all the antibrachial extensors, comprising *mm. brachioradialis* (sometimes supplied by a separate branch), *extensores carpi radialis longus* and *brevis*, *abductor pollicis longus*, *extensor digitorum communis*, *extensor pollicis longus*, *extensores digitorum II*, *III*, *IV et V proprii*, *extensor carpi ulnaris*, and *supinator.*

C. Nerves of the ventral group

In respect to the connection between the roots of T1 and T2 it is impossible to determine grossly the components that receive fibers from the latter. According to the experiments of Sherrington (1898) the part of T2 going to the plexus contributes motor branches to only the median and ulnar nerves. The distribution is as follows:

1. *Nn. thoracales anteriores* (lateral and medial cords) comprise the anterior thoracic loop. The lower end of this arises from C8 and T1, and the other from the three upper nerves of the plexus, either by a single branch, or by two (one from C7) which fuse. From this loop are given off two or three upper twigs which go to the *m. pectoralis major.* Then

successively there occur a lower branch to the *m. pectoralis minor*, another to the *m. pectoralis abdominalis*, and a final, lowermost branch to the *m. panniculus carnosus*. In addition, from the latter nerve, there may be an anastomosing branch to the lateral division of the third intercostal nerve.

2. *N. subclavius* (lateral cord) has close relationship with the nn. thoracales anteriores. It arises from the trunk formed by the juncture of C5 and C6, and innervates the *m. subclavius*.

3. *N. musculocutaneus* (lateral cord) arises from C5, C6, and C7 and passes with the other appendicular nerves to the medial side of the upper arm. Proximally, in the axillary space, it breaks up into two small and two larger branches, the latter of which pass forward between the m. coracobrachialis medius (deep to it) and the tendon of the m. latissimus dorsi. The branches are divisible as follows:

(a) *Rami musculares*. The two smaller branches go directly to innervate the *mm. coracobrachiales profundus* and *medius* respectively, while from the others twigs go to supply the *mm. biceps brachii* and *brachialis*.

Just below the point where branches are given off to the m. brachialis, the n. musculocutaneus usually receives an anastomosing branch from the n. medianus, the two uniting to form the following:

(b) *N. cutaneus antibrachii lateralis*. This becomes subcutaneous from between the mm. biceps and brachialis, above the bend of the elbow, and supplies the skin along the radial border of the flexor surface of the fore arm, mostly upon the radial side.

4. *N. medianus* (lateral and medial cords) is formed by increments from all six nerves of the plexus. It extends down the medial side of the upper arm with the brachial artery and then between the mm. biceps and brachialis. In the brachium it usually gives off an anastomosing branch to the n. musculocutaneus (see above), and at times a small branch innervating the extreme medial part of the *m. brachialis*. (This merely is an indicaton that some of the fibers to the m. brachialis which ordinarily pass by way of the n. musculocutaneus at times reach the muscle by way of the n. medianus.) Passing into the antibrachial muscle-mass between the latter muscle and the m. pronator teres, it continues down the fore arm in a groove upon the deep surface of the m. flexor digitorum sublimis. Just above the wrist it curves around the radial border of the tendons of the latter muscle, attaining a more superficial position, and so enters the hand beneath the volar transverse carpal ligament. It innervates no muscle in the brachium, but in its lower course it gives off the following branches:

(a) *Ramus anastomoticus* (cum n. ulnari). This diverges just above (or even below for a variable distance) the bend of the elbow, passes deep to the superficial head of the m. flexor digitorum profundus, and joins the n. ulnaris at about the middle of the antibrachium.

(b) *Rami musculares*, passing beneath the superficial head of the m. flexor digitorum profundus, innervate all the flexor muscles of the fore arm except the mm. flexor carpi ulnaris and epitrochleo-anconeus; or, in other words, branches supply the *mm. palmaris longus*, *pronator teres*, *flexor carpi radialis*, *flexor digitorum sublimis*, and *flexor digitorum profundus*, including the part representing the flexor pollicis longus of man. Of the deep flexor a radial muscular branch innervates the radial portion of this muscle, and an ulnar branch, diverging from the volar interosseous nerve, the ulnar portion, but no part of the muscle is normally supplied by the ulnar nerve as it is in man and many other mammals.

(c) *N. interosseus antibrachii volaris* is the branch diverging in the upper antibrachium and extending to the interosseous membrane, along which it passes to the deep surface of the *m. pronator quadratus*, which it innervates, and so to the structures of the wrist joint. In its upper course it supplies a branch to the ulnar portion of the *m. flexor digitorum profundus*.

(d) *Ramus cutaneus palmaris* arises from the n. medianus above the wrist and passes along the radial side of the hand to the thumb.

(e) *Nn. digitales volares communes.* Toward the radial side of the palm the n. medianus splits into three branches. All three extend distally as cutaneous nerves to both sides of the first three digits and the radial side of the fourth. In addition the first two (usually) *mm. lumbricales* are innervated by twigs from the middle and ulnar branch, while from the first or radial branch twigs go to innervate the *mm. abductor pollicis brevis*, *opponens pollicis*, and part or all of the *m. flexor pollicis brevis*.

5. *N. ulnaris* (medial cord) arises from C8, T1 and T2 and passes down the medial brachium in its groove between the mm. triceps longus and triceps medialis, covered by the m. dorso-epitrochlearis. It passes over the elbow, between the lateral epicondyle of the humerus and the olecranon, deep to the m. epitrochleo-anconeus, and extends deep to the m. flexor carpi ulnaris. It then runs between that muscle and the ulnar portion of the m. flexor digitorum profundus, and divides just above the pisiform bone. In its course it gives off the following branches:

(a) *Rami musculares.* Just above the elbow a fine filament splits off, which innervates the *m. epitrochleo-anconeus*. In the fore arm it gives rise to two branches, both of which enter the *m. flexor carpi ulnaris* at different levels.

Below this point the n. ulnaris receives a stout anastomosing branch from the n. medianus (see above).

(b) *Ramus dorsalis manus* separates from the main trunk at a variable level and emerges in the distal third of the antibrachium from between the m. flexor carpi ulnaris and the ulna. It there divides into three branches: (1) a partially recurrent one, extending medially and proximally over the ulnar border and anastomosing with the n. cutaneus antibrachii medialis, (2) a median branch supplying the skin mostly toward digits III and IV, and (3) an ulnar branch to the dorsum of digits IV and V.

(c) *Ramus volaris manus superficialis* separates from the next division just above the pisiform. It does not pass beneath the main transverse volar ligament. It innervates the *m. palmaris brevis* and is distributed to both sides of digit V and the ulnar side of digit IV. A branch also anastomoses with the n. digitalis volaris communis medianus.

(d) *Ramus volaris manus profundus* passes deep to the transverse volar ligament of the carpus. It curves radialward in the palm and supplies those *volar muscles* not innervated by the median nerve.

6. *N. cutaneus brachii et antibrachii medialis* (medial cord) arises singly from C8 and T1 (and doubtless T2 as well). In the region of the shoulder this splits into a brachial branch, supplying mostly the skin over the anterior half of the medial arm (the posterior half, over the m. dorsoepitrochlearis, is supplied by the n. intercostobrachialis, usually from the second intercostal nerve, with which there appears to be no anastomosis), and an antibrachial branch, emerging subcutaneously near the elbow from between the biceps and triceps muscle groups and innervating the skin of the medial fore arm.

RAMI VENTRALES NN. THORACALES

These follow the intercostal spaces, except for the twelfth, which passes below the last rib. The lower nerves of the series follow a course that is more caudal than transverse, while the upper ones run in a direction that is almost transverse. The ventral rami of the thoracic nerves supply short muscular branches to the *mm. intercostales*, *transversus thoracis*, *scalenus longus* and *sternocostalis*, and to the *muscles of the lateral and ventral walls of the abdomen*. Each intercostal nerve may be considered to consist of ventral and lateral divisions, which become cutaneous to supply the contiguous skin.

The cutaneous twigs of the ventral divisions pierce the superficial muscles close to the sternum and the linea alba, and are small and rather irregular, especially in the abdomen.

The cutaneous twigs of the lateral divisions are larger and well developed. Each emerges subcutaneously and sends twigs dorsally and ventrally. That of the first intercostal space is probably not cutaneous. That of the second supplies the skin of the medioposterior part of the upper arm (*n. intercostobrachialis*). The third and often the fourth pierce the border of the pectoralis muscle complex. The remainder emerge in the vicinity of the ventral margins of the digitations of the m. serratus anterior, or, more caudally, pierce the abdominal muscles.

PLEXUS LUMBOSACRALIS

(Fig. 110)

In the macaque it is more convenient to consider the lumbar and sacral plexuses as a single unit. This consists of the rami ventrales of the lumbar and sacral nerves, divisible, as in the case of the other spinal nerves, into dorsal and ventral divisions. It is somewhat more difficult than in the case of the cervicobrachial plexus to determine with exactitude the derivation of each branch of the plexus. Similarly the scheme of plexus formation is quite different from that of the brachial plexus, for there are no structures that may be considered as strictly representing trunks, major divisions, and cords, and the actual separation into dorsal and ventral strata is much more difficult of accomplishment.

The plexus is composed of the ventral rami of all seven lumbar and the first two sacral nerves. Cranially it emerges from between the mm. psoas major and quadratus lumborum, while the caudal part lies dorsal to the flexor muscles of the tail. As with the brachial plexus no attempt is made to allocate the shortest branches to the dorsal or the ventral group.

A. Rami musculares

Rami musculares, short and deep, from the roots of the lumbar nerves go to *mm. psoas major* and *minor*, and *quadratus lumborum*.

B. Nerves of the dorsal group

1. *N. cutaneus femoris lateralis* (fig. 111), from L3 and L4, or L3, L4 and L5. This passes through the m. psoas major and runs to the groin where, midway between the inguinal ring and the anterior superior spine of the ilium, it pierces all three layers of the abdominal muscles and is distributed to the skin of the anterior part of the thigh.

2. *N. femoralis* is derived from L3, L4 and L5, or L4 and L5 alone (according to Sherrington (1892), at times also from L6). (Although the n. saphenus and the other cutaneous branches to the posterior half of the thigh are presumably derived from the ventral half of the plexus, the entire femoral nerve is here included for convenience.) It passes with the femoral vessels to the inner side of the thigh, where it breaks up into its terminal branches. These may be subdivided as follows:

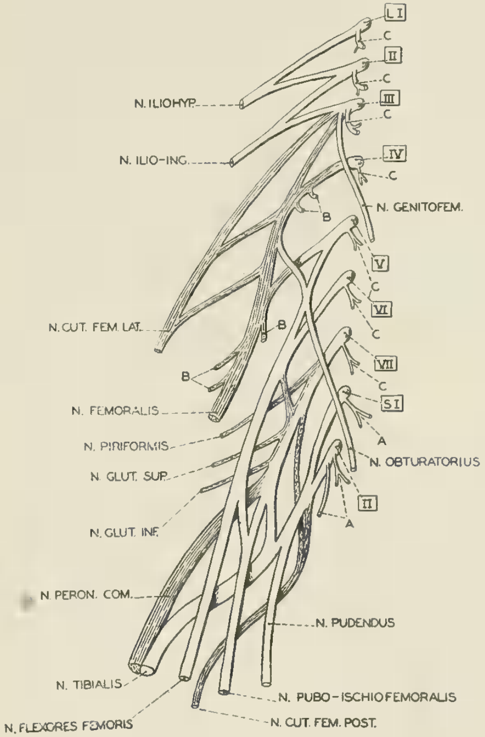

Fig. 110. Dissection of a lumbosacral plexus. A, branches to the caudal flexor muscles; B, branches to mm. iliacus and psoas major; C, branches to mm. psoas major, psoas minor and quadratus lumborum.

(a) *Rami musculares*, short and deep, to the *mm. psoas major* and *iliacus*.

(b) *Rami cutanei anteriores*, to the skin of the medioposterior aspect of the thigh, superficial to the m. sartorius, and to the medial knee. Or these branches may really be considered as part of the next nerve.

(c) *N. saphenus* (fig. 111), the true continuation of the femoral nerve, extends subcutaneously down the medial thigh and innervates the skin of the medial and anterior aspects of the lower leg. It passes partly deep to the m. sartorius.

(d) *Rami musculares*, in the extreme upper thigh, extend by one or two separate branches to the *m. sartorius*, to the *m. pectineus* (passing beneath the femoral vessels), and between the m. rectus femoris and the m. vastus medialis to the quadriceps femoris muscles (*mm. rectus femoris* and the *3 vasti*).

3. *N. piriformis*, from L7, separates from the cord within the pelvis and enters the deep belly of the *m. piriformis* near its origin.

4. *N. gluteus superior*, from (L4?), L5, L6, and L7, or L6 and L7 alone, emerges laterally from beneath the cranial border of the m. piriformis, passes between the *mm. glutei medius* and *minimus*, with branches to both muscles, and then, upon the anterior hip, to the *m. tensor fasciae latae*.

5. *N. gluteus inferior*, also from L5, L6, and L7, or L6 and L7 alone, emerges laterally from beneath the caudal border of the mm. piriformis and gluteus medius to enter the *m. gluteus maximus* along its posterior border.

6. *N. peroneus communis* exhibits various degrees of separation from the n. tibialis, even to the extent that there may be no true n. ischiadicus. It arises from L5, L6, and L7, and sometimes from L4 as well. With the n. tibialis (the two forming the so-called n. ischiadicus) it passes to the lateral thigh and then distalward, between the mm. biceps, semimembranosus and the adductor mass. In the shank the main trunk of the nerve passes lateral to the lateral head of the m. gastrocnemius and then deep between the fibular and tibial orgins of the m. peroneus longus. In its course it gives off, after almost exactly the same pattern as in man, the following branches:

(a) *N. cutaneus surae lateralis* (fig. 111) separates from the common trunk in the middle of the thigh and a number of cutaneous twigs pierce the insertional end of the m. biceps femoris. The lateral calf and upper shank are thus supplied.

(b) *N. peroneus profundus*, which splits from the common stem behind the knee, passes down the lower leg deep to the peroneal muscles and *m. extensor digitorum longus*. It gives off branches to the latter, the *m. extensor hallucis longus*, and *m. tibialis anterior*. It passes beneath the dorsal transverse crural ligament, between the mm. extensores digitorum longus and hallucis longus, and deep to the *m. extensor digitorum et hallucis brevis*, sending rami musculares to the last, and cutaneous branches to the medial digits.

(c) *N. peroneus superficialis*, from the common trunk in the upper shank, takes the form of several rami musculares to the *mm. peronei*, and the n. cutaneus pedis dorsalis medialis. The latter extends between the tibial head of the m. peroneus longus and the m. extensor digitorum longus, and then subcutaneously to distribution over the lateral side of the dorsum of the foot.

(d) *N. cutaneus pedis dorsalis intermedius* diverges from the common trunk below the knee and is entirely subcutaneous in its course, extending to the rear of the lateral malleolus and so to the skin upon the lateral side of the dorsum of the foot.

7. *N. cutaneus femoris posterior* (fig. 111), supposedly a mixed nerve with some ventral elements, arises from L7, S1 and (probably) S2. It passes with the rest of the nerves of the posterior hip from beneath the border of the m. piriformis, and becomes subcutaneous between the m. gluteus maximus and the lateral margin of the tuber ischiadicum. Thence it is distributed to the ischial callosity and to the skin of the posterior buttock and the lateral part of the thigh. There is no separate posterior cluneal nerve.

C. Nerves of the ventral group

1. *N. iliohypogastricus* and

2. *N. ilio-inguinalis*. The former of these comes from L1 and L2, and the latter from L2 and L3, and in the rhesus macaque they exhibit a simpler pattern than in man. They emerge from between the mm. quadratus lumborum and psoas major and send sensory and muscular twigs to the *lateral and ventral parts of the lower abdomen*.

3. *N. genitofemoralis* (fig. 111), from L3, or L2 and L3, pierces the m. psoas major and extends as a single fine nerve between that muscle and the peritoneum, near the midline. It divides near the level of the inguinal ring into two branches, which are distributed (1) to the skin about the femoral ring (lumbo-inguinal branch) and (2) to the *m. cremaster* and to the scrotum in the male, and vulva in the female (external spermatic branch).

4. Cutaneous branches to the posteromedial part of the leg that are derived from the n. femoralis are believed to belong to the ventral part of the plexus, but have been described with the dorsal group.

5. *N. obturatorius*, from L3, L4 and L5, or L4, L5 and L6, passes along the medial surface of the tendon of the m. psoas minor, between the seminal vesicles and the pubic bone in the male. It passes between the m. iliocaudalis and m. pubocaudalis, deep (external) to the latter muscle, and, piercing the m. obturator internus, goes through the obturator fora-

men and supplies the *mm. adductores*, *gracilis*, and *obturator externus*, also giving off some cutaneous branches to the medial thigh.

N. obturatorius accessorius does not occur.

6. *N. flexores femoris* is the term employed for the separate nerve which in the rhesus macaque innervates the hamstring muscles, although in other mammals these muscles are frequently supplied by branches of the n. tibialis. It arises from L4, L5 and L6, or even as low as L6, L7 and S1, and accompanies the n. tibialis to the upper part of the thigh, where it gives off rami musculares to the deep bellies of the *mm. semitendinosus*, *semimembranosus*, and *biceps femoris*.

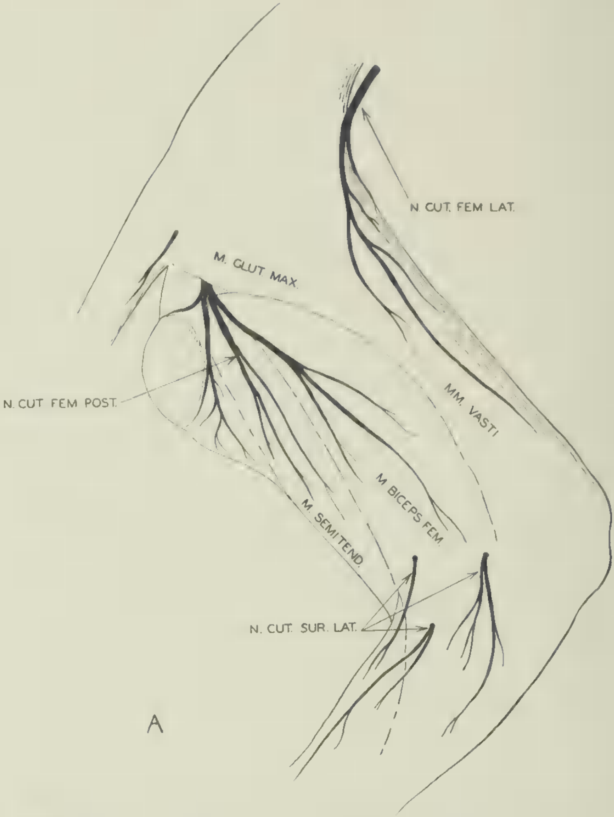

FIG. 111. Dissection of the cutaneous nerves of the right thigh and leg. A, lateral view; B, medial view.

7. *N. tibialis* is derived from the five nerves from L5 to S2. (Accord-

ing to Sherrington (1892), the contribution from S2 may be absent.) In many mammals it is a component of the great sciatic (ischiadic) nerve, but in the rhesus monkey it is readily separable from the n. peroneus communis, which it accompanies down the thigh. At the bend of the knee it divides into a number of branches, most of which enter the calf between the two heads of the m. gastrocnemius. It then extends down the back of the lower leg between the triceps surae and the deeper flexors of the calf, to the medial malleolus, slightly above which it divides into the two plantar nerves. In its course it gives off the following branches:

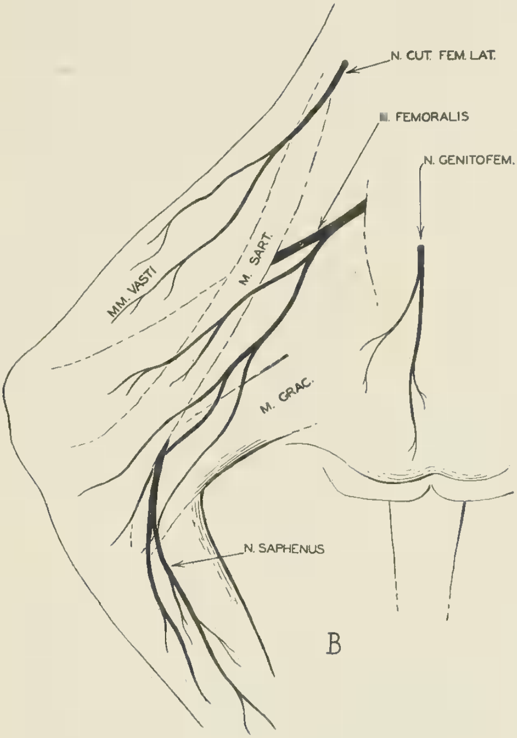

Fig. 111, B

(a) *N. cutaneus surae medialis* separates in back of the knee and extends down the center of the posterior calf, below which its course is more lateral. Here it is known as the n. suralis. It passes behind the lateral malleolus and its twigs are distributed to the skin of the heel (rami calcanei laterales) and the lateral margin of the foot (n. cutaneus dorsalis lateralis). It sends a large ramus anastomoticus to join the lateral plantar nerve at the level of the medial malleolus.

(b) *Rami musculares*, dividing in the politeal space, pass between the two heads of the *m. gastrocnemius.* They supply these, as well as the *mm. soleus*, *plantaris*, *popliteus*, *peroneotibialis*, and send other branches to the *mm. flexor digitorum tibialis*, *flexor digitorum fibularis*, and *tibialis posterior.*

(c) *N. plantaris medialis* separates above the medial maleolus. It passes beneath (dorsal to) the origin of the m. abductor hallucis and sends rami musculares to the *mm. flexor digitorum brevis* (both heads), *abductor hallucis*, *flexor hallucis brevis* and *lumbricales* of (usually) toes *II* and *III*, as well as sensory twigs to the medial plantar surface.

(d) *N. plantaris lateralis* passes from behind the medial malleolus, beneath the m. abductor hallucis, to the plantar surface of the foot. It extends lateralward between the superficial and deep heads of the m. flexor digitorum brevis, and sends rami musculares to the *mm. quadratus plantae*, *abductor digiti quinti* and (when present) *abductor ossis metatarsi quinti.* It then splits into superficial and deep divisions. The former (ramus superficialis) sends rami musculares to the *m. flexor digiti quinti brevis* and (at times) to the *mm. interossei* of the most lateral interosseous space, and gives off cutaneous branches to the lateral two-thirds of the planta. The deep division (ramus profundus) passes between the *mm. contrahentes digitorum* and the *mm. interossei*; it sends rami musculares to all of the muscles of these two groups, to the *mm. lumbricales* of (usually) toes *IV* and *V*, and (at times) to the *m. flexor digiti quinti brevis* as well, and ends medially in rami musculares in the two heads of the *m. adductor hallucis.*

8. *N. pubo-ischiofemoralis*, from L4 (probably), L5, L6 and L7, accompanies the n. ischiadicus to the outside of the pelvis, and innervates the *mm. obturator internus*, *gemelli* and *quadratus femoris.* (Fibers of this nerve component may be partly bound up with the n. flexores femoris.)

9. *N. pudendus* arises from L7 and S1, or from S1 nd S2, and the plan of distribution is considerably simpler than in man. The branches follow the ischiadic complex of nerves emerging from beneath the posterior border of the m. gluteus maximus close to the tail. They may be termed as follows:

(a) *Nn. scrotales posteriores* pass superficially near the midline to the skin of the posterior scrotum in the male (labia in the female).

(b) *Rami musculares superficiales* are associated with the last, and innervate the *mm. sphincter ani externus*, *bulbocavernosus*, *ischiocavernosus*, *levator penis* and *sphincter urethrae membranaceae* in the male, and the *mm. sphincter cloacae* (and its derivatives) and *ischiocavernosus* in the female.

(c) *Nn. haemorrhoidales inferiores* (at times one separate nerve) are distributed to the skin about the anus.

(d) *N. dorsalis penis* (*dorsalis clitoridis* in the female) passes deep immediately posterior to the anus and then follows the dorsum of the penis (clitoris), the skin of which it supplies.

10. *Rami musculares*, from S1 and S2, pass to the ventral caudal muscles (*mm. flexor caudae longus*, *flexor caudae brevis*, *ischiocaudalis*, *iliocaudalis*, and *pubocaudalis*).

NERVI CAUDALES

In the rhesus macaque there are four pairs of caudal nerves, which it will not be found feasible, in practice, to differentiate into dorsal and ventral components. Their branches (together with S3) innervate the skin and musculature of the entire tail.

Rami Dorsales

The rami dorsales of the spinal nerves are distributed to the skin and muscles of the back proper. As a rule they divide into medial and lateral branches, one of which is chiefly muscular and the other exclusively cutaneous.

Ramus dorsalis n. cervicalis I comprises the *n. suboccipitalis.* It is larger than the anterior ramus and is solely muscular. It innervates the *extreme superior divisions of the intrinsic back musculature* and anastomoses with the second cervical nerve.

Ramus dorsalis n. cervicalis II. The lateral and part of the medial ramus of this nerve supply muscular twigs to the *longer*, *cervical components of the intrinsic back musculature*, and anastomose with the first and third cervical nerves. The remainder of the medial ramus constitutes the *n. occipitalis major.* This approaches the midline beneath the m. semispinalis capitis, pierces the overlying muscles, and sends branches to the skin over the back of the head. It is relatively smaller than in man.

Ramus dorsalis n. cervicalis III. This differs from the lower cervical nerves in that its medial division, constituting the sensory *n. occipitalis tertius*, is distributed in a cranial direction to the occipital region of the head, with the n. occipitalis major.

Of the remainder of the dorsal rami of the spinal nerves the medial branches as far as the seventh or eighth thoracic are cutaneous and emerge subcutaneously immediately adjacent to the midline. The lateral branches of these nerves are accordingly muscular. In the lower thorax and in the lumbar region, however, this condition is reversed, the medial branches being muscular and the lateral branches cutaneous, the latter occurring several centimeters away from the midline, the most caudal being but a short distance from the ilium. All of these branches are relatively small.

Comparative anatomy. In the lower primates (especially in prosimians and New World monkeys) the cervical and brachial plexuses are isolated from one another by a considerable intermediate zone. A phylogenetic shortening of the interval between the two plexuses has occurred in the higher primates. This shortening is apparently the result chiefly of an upward spreading of the brachial plexus.

The ventral ramus of the second thoracic nerve not infrequently contributes to the formation of the brachial plexus (leading to the formation of a so-called "postfixed" type of plexus) in primates. This contribution to the plexus from n. thoracalis II is the rule in Old World monkeys (it is constantly present and of considerable size in the macaque). It occurs not infrequently in man, and has also been encountered in some anthropoid apes, New World monkeys and prosimians.

Anastomoses between the musculocutaneous and median nerves in the upper arm, and between the median and ulnar nerves in the fore arm, are not rare in man, and occur frequently in other primates. The musculocutaneous nerve may be absent as a distinct structure, its fibers in such instances being bound up with those of the median nerve. The median and ulnar nerves may be united in the upper arm to form a common trunk practically as far as the elbow.

The lumbosacral plexus exhibits various degrees of "prefixation" and "postfixation" in respect to the origins of its resultant nerves. These types of lower limb plexus show fairly close generic correlation with the number of presacral vertebrae, and are probably intimately associated with a phylogenetic shortening or lengthening of the trunk. The process of "prefixation" of the lumbosacral plexus is most extreme among primates in the orang-utan, in which the presacral portion of the vertebral column has undergone the greatest numerical reduction; while the primate extreme of the opposite condition of "postfixation" occurs in the lorisine lemurs, in which the presacral column has experienced the greatest numerical lengthening.

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CHAPTER XVII

THE AUTONOMIC NERVOUS SYSTEM

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The autonomic nervous system consists of two main divisions, viz., the *sympathetic*, connected with the central nervous system through the thoracic and upper lumbar spinal nerves, and the *parasympathetic*, connected with the central nervous system through the third, seventh, ninth, tenth and eleventh cranial and the seventh lumbar and first and second sacral nerves. The sympathetic system includes the sympathetic trunks with the nerves arising from them and certain ganglia associated with the abdominal viscera, with the fibers arising in these ganglia. The parasympathetic system includes the autonomic ganglia which are functionally related to the cranial and to the lowermost lumbar and the sacral nerves and the nerve fibers arising in these ganglia. The nerves belonging to the two divisions of the autonomic system therefore are not distinct anatomically, but intermingle particularly in the cephalic region and the plexuses associated with the visceral organs.

SYMPATHETIC TRUNKS

Each sympathetic trunk extends along the ventrolateral aspect of the vertebral column from the base of the cranium to the tail (fig. 112). It is made up of a series of ganglia connected by longitudinal fibers which in general are segmentally arranged, except in the cervical region, and are connected with the spinal nerves through communicating rami.

The cervical portion of the sympathetic trunk includes the superior, middle (sometimes absent) and inferior cervical ganglia (fig. 113A). The inferior cervical and first thoracic ganglia commonly are fused and constitute the stellate ganglion.

THE SUPERIOR CERVICAL GANGLION is a spindle-shaped body of variable size lying in front of the transverse processes of the second and third vertebrae, medial to the internal carotid artery and in general parallel to the nodose ganglion of the vagus nerve (fig. 113A). From its upper pole, two nerves, viz., the internal carotid and jugular, extend into the cephalic region. The internal carotid nerve consists of a variable number

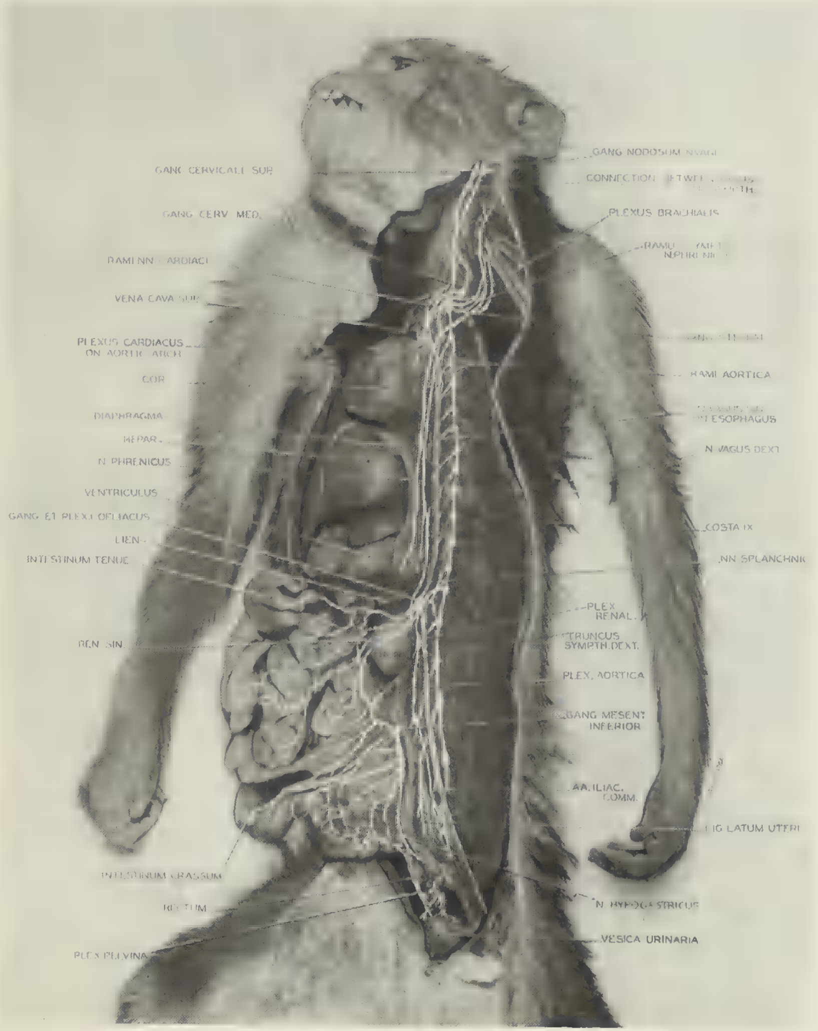

FIG. 112. Dissection showing the autonomic nervous system of neck and trunk and its relation to the viscera.

of strands of nerve fibers which join the internal carotid artery and interlace with one another around it to form the internal carotid plexus. The jugular nerve consists of two rami, one of which enters the jugular foramen and joins the jugular ganglion; the other either passes through the petrosal ganglion or over it and joins the tympanic plexus. The superior cervical ganglion is connected with the nodose ganglion by one or more short rami and with the hypoglossal nerve by at least one slender ramus. It sends a communicating ramus to each of the upper three or four cervical nerves. Several slender rami are supplied to the pharynx, one or more to the esophagus, one or more join the plexus on the external carotid artery, and at least one slender descending ramus joins the plexus on the common carotid artery.

Continuing downwards from the inferior pole of the superior cervical ganglion, the sympathetic trunk is closely associated with the vagus nerve and lies along the lateral aspect of the common carotid artery. On the right side one or more rami arising either from the lower pole of the superior cervical ganglion or the sympathetic trunk at a somewhat lower level tend downwards and join the vagus nerve. One or more anastomosing rami also connect the sympathetic trunk and vagus nerve at about the level of the fifth cervical vertebrae. On the left side, the superior cervical sympathetic and nodose ganglia are joined together by a heavy ramus from which a slender branch joins the superior laryngeal nerve. Riegele (1926) described another slender ramus passing downwards from the connecting ramus parallel to the sympathetic trunk and giving off branches both to the latter and the vagus nerve, and communicating rami to the second and third cervical nerves. Such a descending ramus could not be demonstrated with certainty in our dissections. An anastomosis between the sympathetic trunk and the vagus nerve at about the level of the fifth cervical segment has been observed in some cases.

THE MIDDLE CERVICAL GANGLION appears as a slight enlargement in the course of the sympathetic trunk just above the subclavian artery. Between the middle cervical and stellate ganglia, the fibers of the sympathetic trunk pass in part on one side and in part on the other side of the subclavian artery, thus forming a loop, the ansa subclavia, around this vessel. Riegele described a small ganglion on the anterior limb of this loop on the right side, from which a slender ramus joins the vagus. He proposed that this ganglion be designated the ganglion supremum.

Communicating rami arising from the middle cervical ganglion join the fifth and sixth (sometimes also the fourth) cervical nerves. A cardiac nerve also arises from the middle cervical ganglion or directly from the cervical sympathetic trunk above it. This nerve probably includes fibers which descend from the superior cervical ganglion. A separate cardiac nerve arising from the latter ganglion has not been found in our dissections. Slender rami arising from the middle cervical ganglion or the cervical sympathetic trunk also join the plexuses on the common carotid and vertebral arteries. One or more rami also extend medianwards and anastomose with corresponding rami from the opposite side. Rami arising from the ansa subclavia join the recurrent nerve and the plexus on the subclavian artery.

The stellate ganglion typically is located on the anterior aspect of the head of the first rib. It is irregular in form and differs both in form and size on the two sides. The inferior cervical cardiac nerve commonly arises from the medial aspect of this ganglion. In some instances, all the cervical sympathetic cardiac nerves unite to form a single trunk, particularly on the left side. Gray communicating rami arising from the stellate ganglion join the seventh and eighth (sometimes also the sixth) cervical and first thoracic nerves. This ganglion also is connected with the first thoracic nerve by a white communicating ramus. Slender rami from the stellate ganglion also join the plexuses on the subclavian and vertebral arteries.

Throughout the thoracic region, the sympathetic trunk lies between the pleura and the necks of the ribs, and exhibits a ganglion in every segment (except the first). Each thoracic ganglion is connected with the corresponding spinal nerve by a white and a gray communicating ramus. In some instances, the white and gray rami may be recognized as separate bundles, the gray ramus joining the spinal nerve proximal to the white ramus. In other instances, the gray and white communicating rami constitute a single bundle. Occasionally a sympathetic ganglion is connected with the corresponding spinal nerve by more than two rami. Slender rami arising from the medial aspects of the sympathetic ganglia or the interganglionic portions of the sympathetic trunk in the upper four or five thoracic segments pass directly into the cardiac plexus. These have been called the thoracic cardiac nerves. Still other rami join the esophageal and pulmonary plexuses and the plexus on the descending aorta. A few medial rami also pass across the vertebrae and anastomose with corresponding rami from the opposite side.

The splanchnic nerves arise mainly from the last thoracic and first two or three lumbar ganglia. Greater, lesser and least splanchnic nerves, as commonly found in man, cannot be clearly recognized. Three nerves arising from the lower thoracic and upper lumbar portions of the sympathetic trunk join the celiac plexus. The first and second of these, arising from the last thoracic and first lumbar ganglia respectively, sometimes exhibit one or more anastomoses, and in some instances unite to form a single nerve. The third, arising from the second or third lumbar segment of the sympathetic trunk, enters the celiac plexus, but also sends branches to the renal plexus (fig. 113B).

In passing from the thorax into the abdomen, the sympathetic trunk either pierces the diaphragm or passes behind it. In the lumbar region, it lies upon the bodies of the vertebrae in front of the lumbar vessels. Five or six ganglia usually are present in the lumbar region, but there may be a larger number. All the lumbar nerves are connected with the sympathetic trunk by communicating rami. Of these rami probably only those connected with the upper three and the lowest lumbar nerves include preganglionic fibers. The arrangement of the communicating rami in this region is somewhat irregular. In some instances, one ramus divides so as to send a branch to each of two adjacent nerves. In other instances, a single spinal nerve is joined by two or more rami arising separately from the sympathetic trunk. The communicating rami in this region usually lie close to the bodies of the vertebrae. In some instances, they pierce the psoas major muscle. Rami arising from the lumbar portion of the sympathetic trunk at irregular intervals join the aortic plexus. Several larger rami join the inferior mesenteric plexus and several small ones pass medianwards and anastomose with corresponding rami from the opposite side.

Continuing into the pelvis, the sympathetic trunk assumes a position on the pelvic surface of the sacrum approaching the median plane more closely as it descends. It terminates inferiorly in the upper caudal region. The sacral portion of the sympathetic trunk comprises two or three small ganglia which are somewhat irregularly spaced and diminished in size from above downwards. It is connected with the seventh lumbar and sacral nerves by communicating rami which, however, do not contain preganglionic fibers. Rami of small size arising from the lower lumbar segments of the sympathetic trunk join the pelvic plexus. Several rami also anastomose with corresponding rami from the opposite side.

PREVERTEBRAL PLEXUSES

The cardiac, pulmonary, celiac, hypogastric and pelvic plexuses constitute the major prevertebral plexuses, to which minor plexuses are subsidiary.

THE CARDIAC PLEXUS consists of a superficial and a deep part. The superficial cardiac plexus lies in the concavity of the aortic arch, and is made up mainly of the left cervical sympathetic cardiac nerves (except the inferior) and a cervical cardiac branch of the left vagus. As these nerves approach the heart, they pass over the arch of the aorta and meet on the right side of the ligamentum arteriosum. The cardiac ganglion of Wrisberg, when present, is located at this point. The deep cardiac plexus lies behind the arch of the aorta and in part between the aorta and the pulmonary veins. It is composed of two lateral parts which are quite unlike in composition and distribution. The left portion is made up mainly of fibers derived from the left cervical and thoracic sympathetic cardiac nerves and the inferior cervical cardiac branches of the left vagus. The right portion is made up mainly of fibers derived from the right cervical and thoracic sympathetic cardiac nerves and all the cardiac branches of the right vagus. The right and left portions of the deep cardiac plexus are joined together by transverse strands of nerve fibers. Both portions also are connected with the superficial cardiac plexus.

The coronary plexuses invest the coronary arteries and are continuous with the superficial cardiac plexus. Both coronary plexuses also receive fibers from the deep cardiac plexus.

THE PULMONARY PLEXUSES include an anterior and a posterior pulmonary plexus on either side situated on the anterior and posterior aspects respectively of the roots of the lungs. The anterior pulmonary plexus receives fibers through the pulmonary branches of the vagus, from the corresponding part of the deep cardiac plexus and, on the left side, also from the superficial cardiac plexus. The posterior pulmonary plexus is made up mainly of branches of the vagus and slender rami from the second, third and fourth thoracic sympathetic ganglia.

The CELIAC PLEXUS comprises an extensive meshwork of nerve fiber bundles, two chief ganglia and a variable number of smaller ganglia. It surrounds the celiac artery and the root of the superior mesenteric artery. It is joined by all the splanchnic nerves and several rami of the right vagus (fig. 113 B). The latter doubtless also convey fibers derived from the left vagus through a ramus which joins the right vagus above the diaphragm. The hepatic, splenic and left gastric plexuses, which invest the corresponding branches of the celiac artery respectively, are continuous with the celiac plexus and may be regarded as subsidiary to it. The phrenic plexus arises from the upper part of the celiac plexus and accompanies the inferior phrenic arteries to the diaphragm. It also is joined by rami of the phrenic nerves.

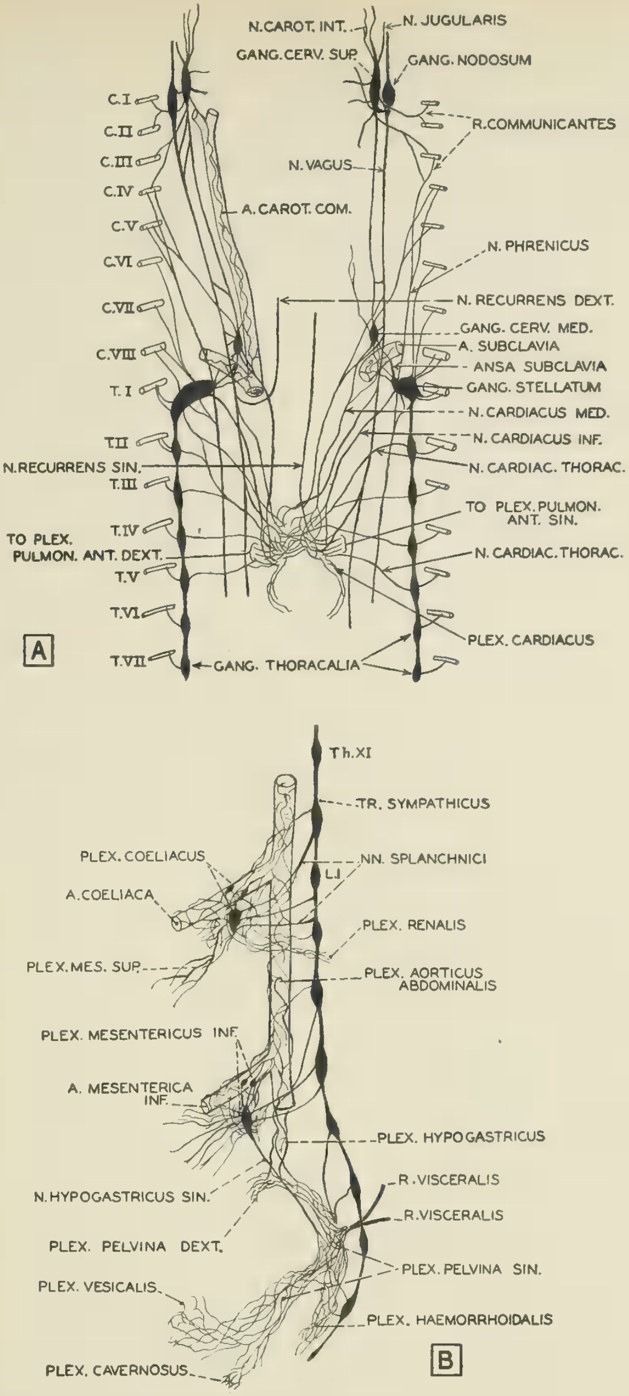

FIG. 113. Semidiagrammatic representation of the autonomic nerves of neck and trunk. A, cervical and thoracic; B, abdominal.

Nerves arising from the celiac plexus also form subordinate plexuses on the abdominal aorta and its branches below the celiac artery. The adrenal plexus is continuous with the celiac plexus and invests the adrenal artery. The renal plexus invests the renal artery. It is made up mainly of nerves derived from the celiac plexus and receives fibers directly from the lowest splanchnic nerve. It also is connected with the adrenal plexus. The superior mesenteric plexus is continuous with the lower part of the celiac plexus and invests the superior mesenteric artery. Near the origin of this artery lies the superior mesenteric ganglion. Through subordinate plexuses on the corresponding branches of the superior mesenteric artery, the superior mesenteric plexus supplies fibers to the pancreas, the small intestine and the first part of the large intestine, including the ascending and transverse portions of the colon. The abdominal aortic plexus invests the abdominal aorta and may be regarded as the continuation downwards of the celiac plexus. It also receives rami directly from the lumbar portions of the sympathetic trunks. Rami arising from the aortic plexus contribute to the spermatic (or ovarian), the inferior mesenteric and the hypogastric plexuses. Slender rami also are distributed to the inferior vena cava. The spermatic plexus extends along the spermatic artery into the spermatic cord. The ovarian plexus extends along the ovarian artery to the ovary. These plexuses also receive rami from the renal plexus. The inferior mesenteric plexus is continuous with the aortic plexus and receives several large rami directly from the sympathetic trunk. It consists of a loose meshwork of fiber bundles, two relatively large ganglia and several small ones. It surrounds the inferior mesenteric artery and gives rise to secondary plexuses on the branches of the artery, viz., the left colic, sigmoid and superior hemorrhoidal plexuses.

THE HYPOGASTRIC PLEXUS is relatively inconspicuous, being made up mainly of filaments derived from the aortic plexus and the lumbar ganglia of the sympathetic trunk. It is situated in front of the last lumbar vertebra and the promontory of the sacrum and between the common iliac arteries and is continuous inferiorly with the right and left pelvic plexuses.

THE PELVIC PLEXUSES (fig. 113 B) are situated along the lateral aspects of the rectum in the male, and the lateral aspects of the rectum and vagina in the female. They are made up of fibers derived from the seventh lumbar and first and second sacral nerves through their visceral rami and from the inferior mesenteric plexus through the hypogastric nerves. They also are continuous with the hypogastric plexus and receive a few small rami from the lower lumbar segments of the sympathetic trunks. The hypogastric nerve on either side is a relatively large compact bundle of fibers extending from the inferior mesenteric plexus directly into the pelvis. Each pelvic plexus gives rise to subordinate plexuses on the hypogastric artery and its branches, viz., the middle hemorrhoidal, vesical, prostatic or uterine and vaginal plexuses, through which the pelvic viscera are supplied.

THE ENTERIC PLEXUSES, viz., the myenteric and submucous plexuses, are located in the wall of the digestive tube throughout nearly its entire length. They are made up mainly of the enteric neurons, the cell bodies of which are located in the ganglia of the myenteric and submucous plexuses respectively. Those of the former plexus lie between the longitudinal and circular muscle layers; those of the latter, in the submucosa. The extrinsic nerves of the digestive tube also contribute fibers to these plexuses.

CEPHALIC SYMPATHETIC PLEXUSES

The cephalic sympathetic plexuses represent the extension of the sympathetic trunk into the cephalic region. Slender rami arising mainly from the upper pole of the superior cervical sympathetic ganglion join the internal and external carotid arteries (fig. 114). Those which join the internal carotid artery become closely applied to this artery as it enters the carotid canal in the temporal bone. At a somewhat higher level, they become separated into a lateral and a medial division. The lateral division gives rise to the internal carotid plexus which invests the internal carotid artery. This plexus gives off communicating branches to the abducens nerve and semilunar ganglion. It also gives rise to the deep petrosal nerve which joins the greater superficial petrosal to form the nerve of the pterygoid canal. The latter terminates in the sphenopalatine ganglion. The caroticotympanic nerve also arises from the internal carotid plexus and joins the tympanic plexus. The medial division gives rise to the cavernous plexus on the cavernous sinus. This plexus gives off communicating branches to the oculomotor, trochlear and ophthalmic nerves and the ciliary ganglion. It also sends fibers to the hypophysis.

The tympanic plexus is situated on the medial wall of the middle ear. It is made up mainly by the caroticotympanic nerve and a tympanic ramus derived from the petrosal ganglion. It supplies fibers to the mucous membrane of the tympanum, mastoid cells and auditory tube. It also gives rise to a slender ramus which joins a branch of the genicular ganglion of the nervus intermedius to form the lesser superficial petrosal nerve, which joins the otic ganglion.

The sympathetic rami which join the external carotid artery give rise to the external carotid plexus. This plexus invests the external carotid artery and forms subordinate plexuses on its branches, viz., the middle meningeal and external maxillary plexuses, which give off branches to the otic and submaxillary ganglia respectively.

The external carotid plexus also is continuous with the common carotid plexus, on the common carotid artery. The latter plexus is made up in part of fibers derived from the middle cervical and stellate sympathetic ganglia. Some fibers derived from these ganglia probably continue upwards in the plexuses on the internal and external carotid arteries.

CEPHALIC AUTONOMIC GANGLIA

THE SUBMAXILLARY GANGLION. This is a small ganglion closely associated with the lingual nerve, and located within the submaxillary gland between this nerve and the submaxillary duct. Its preganglionic (motor root) fibers are derived from the facial nerve via the chorda tympani which joins the lingual nerve near the angle of the mandible. Its sensory root is made up mainly of fibers derived from the nervus intermedius which reach the ganglion through a short ramus of the lingual nerve. A slender ramus derived from the plexus on the external maxillary artery joins the ganglion as its sympathetic root (fig. 114). Some peripheral rami arising from the submaxillary ganglion join the lingual nerve; others run directly to the submaxillary gland and its duct.

THE OTIC GANGLION. This is a very small ganglion located on the medial aspect of the mandibular nerve just below the foramen ovale. It receives both preganglionic (motor root) and sensory (sensory root) fibers from the glossopharyngeal nerve via the lesser superficial petrosal nerve. Its sympathetic root is derived from the tympanic plexus and the plexus on the middle meningeal artery (fig. 114). Rami arising from the otic ganglion join the nerve of the pterygoid canal, the auriculotemporal nerve, the chorda tympani, and the tensor tympani and tensor veli palatini muscles.

THE SPHENOPALATINE GANGLION. This is a small flattened ganglion located deeply in the sphenopalatine fossa and close to the sphenopalatine foramen. It is closely associated with the maxillary nerve and connected with the latter by two or more short rami. It receives both preganglionic (motor root) and sympathetic (sympathetic root) fibers through the nerve of the pterygoid canal. The preganglionic fibers are components of the facial nerve which join the nerve of the pterygoid canal via the greater superficial petrosal nerve. The sympathetic fibers are derived from the internal carotid plexus and join the nerve of the pterygoid canal via the deep petrosal nerve. Sensory components of the maxillary nerve join the sphenopalatine ganglion through the rami connecting it with that nerve (fig. 114).

The following peripheral rami arise from the sphenopalatine ganglion. The orbital rami, one or more in number, pass upwards through the orbit. The nasopalatine nerve passes to the mucous membrane of the hard palate and the roof and septum of the nose. The posterior superior lateral nasal nerve passes to the mucous membrane of the lateral wall of the nasal cavity. Three palatine rami, viz., the anterior, middle and posterior palatine nerves, reach the palate through the palatine canals. A pharyngeal ramus passes backwards to the mucous membrane of the roof of the pharynx.

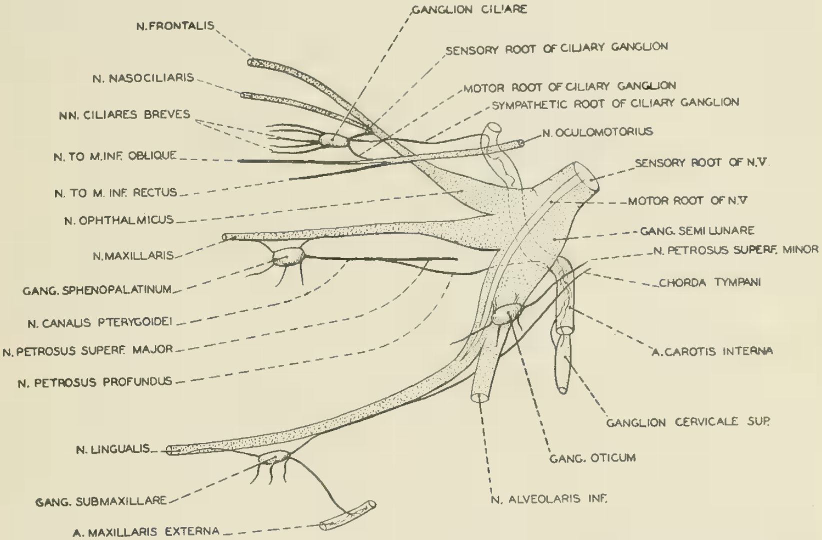

Fig. 114. Diagrammatic illustration from medial aspect of cranial autonomic ganglia in relation to cranial nerves.

The ciliary ganglion. This is a small ganglion located in the posterior portion of the orbit, between the optic nerve and the lateral rectus muscle. It receives preganglionc (motor root) fibers via a short ramus which connects it with the inferior division of the oculomotor nerve, sensory (sensory root) fibers via the nasociliary branch of the ophthalmic nerve and sympathetic (sympathetic root) fibers via a slender ramus derived from the cavernous plexus (fig. 114). A variable number of slender rami, the short ciliary nerves, arise from the ciliary ganglion and approach the eyeball by passing forwards above and below the optic nerve.

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Chapter XVIII

THE EYE AND THE EAR

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The Eye and Associated Structures

The eyeball, together with its associated structures, the extrinsic muscles of the eye, the orbital connective tissue, the lacrimal gland and the eyelids, lie in the orbital fossa of the head.

THE CONTENTS OF THE ORBIT

The bony framework of the orbital fossa is lined by a dense connective tissue membrane, the periosteum or *peri-orbita.* At the margin of the orbit this peri-orbita is continuous with the periosteum lining the bones of the face, but it also sends a septum, the septum orbitale, into the eyelids. Posteriorly the fossa has an opening through which the optic nerve enters. Here the peri-orbita becomes continuous with the dura. The structures within the orbit such as the eyeball, muscles, nerves and vessels are covered by *orbital fascia.* Wherever this fascia comes in contact with the peri-orbita it fuses with it. The spaces between the orbital fascia are filled with lobules of fat which are supported by connective tissue septa of the orbital fascia. The orbital fascia which lines the posterior part of the eyeball, as far anterior as the insertion of the ocular muscle, is described as loosely attached to the eyeball by fine septa and is known as *ocular fascia.* The spaces between these fine septa which are filled with fluid collectively form the space of Tenon, and the ocular fascia forms the capsule of Tenon. In the rhesus monkey the capsule of Tenon and the space of Tenon are not distinctly formed. The ocular fascia is a very loose connective tissue which fuses insensibly with the sclera of the eyeball, and the space of Tenon is therefore not seen even in histological sections. Histological sections, however, show a definite space and capsule around the optic nerve.

THE EYELIDS

These are two folds of skin, one above and one below, which when closed cover the orbital fossa and its contents. When the skin is carefully removed on their outer surface the muscle of the eyelids, *m. orbicularis oculi* (fig. 54), can be seen. On removing this muscle and the associated connective tissue some of the content of the eyelids within the orbital fossa is exposed (fig. 115). In the basal part of the eyelids, at the upper and lower margins of the orbital fossa, two masses of fat are seen. These are subcutaneous fat lying between the inner and outer folds of skin which constitute the eyelids. In the upper lateral angle of the orbit there is exposed part of the *lacrimal gland* (fig. 115), which opens by a series of ducts onto the inner surface of the upper eyelid near its lateral margin. Figure 116 also shows the *tarsus* of the upper eyelid. This is a shield-like mass of dense connective tissue which stiffens the eyelids. Within this tarsus are imbedded the *tarsal* or *meibomian glands*, which appear as yellowish streaks radiating from the base to the free margin of the eyelids. The ducts of these glands open in a row along the free margin of the lids. In the lower lid the tarsus is very poorly developed although the glands are prominent.

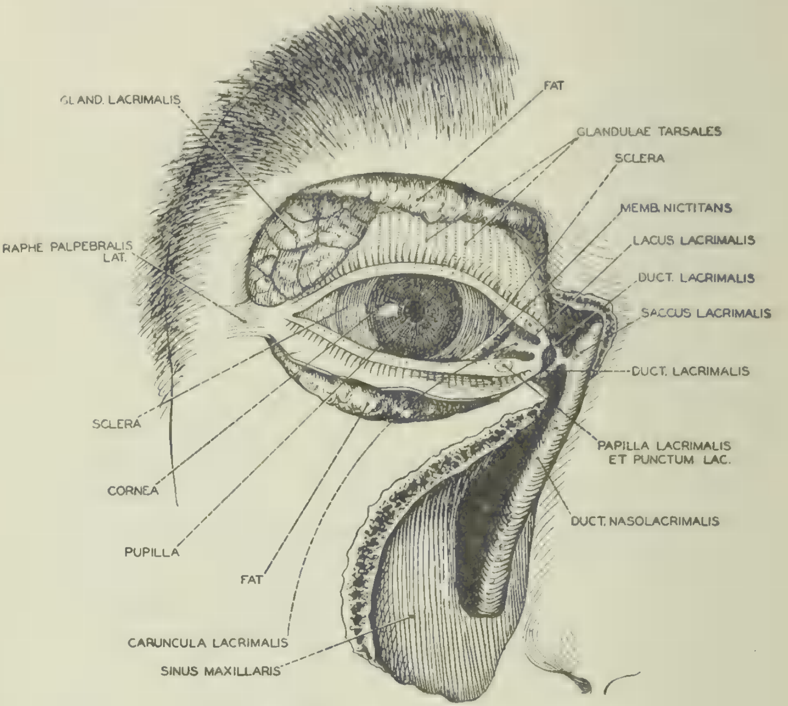

FIG. 115. The right eye, front view.

THE CONJUNCTIVA

The epithelium covering the outer surface of the lids is typical skin epithelium giving rise to hair and sebaceous glands. The hairs, however, are rudimentary except at the outer angle of the lid, where they are stiff and arranged in a row. The covering on the inner surface of the lids loses all characteristics of skin and forms the *palpebral conjunctivum.* At the base of the lids this conjunctivum becomes continuous with the epithelium covering the anterior part of the eyeball, which is known as the *ocular conjunctivum.* The space between the ocular and palpebral conjunctivum is the *conjunctival sac.*

THE LACRIMAL APPARATUS

This consists of the lacrimal gland, which pours its secretion into the conjunctival sac, and a system of ducts which carry this secretion into the nose (fig. 115).

At the inner angle of each eyelid near the medial commissure of the eyelids there is a small papilla, the *lacrimal papilla.* The top of the papilla is directed toward the conjunctival sac. At the top of each papilla is a small opening, the *punctum lacrimale.* Between the eyelids at their nasal angle there is a fold of the conjunctivum projecting like an island into the conjunctival sac, the *caruncula lacrimalis.* Around this island-like fold is a depression, the *lacus lacrimalis.* The caruncula lacrimalis and lacus lacrimalis constitute an apparatus for directing the lacrimal secretion from the conjunctival sac to the puncta lacrimalia and thus into the lacrimal canals. The two lacrimal canals empty into the lacrimal sac, which lies in the groove between the lacrimal bone and the nasal process of the superior maxilla. From this sac the nasal duct passes downward and opens into the inferior meatus of the nose.

THE THIRD EYELID OR NICTITATING MEMBRANE

The nictitating membrane has its origin from the conjunctivum just back of the caruncula lacrimalis and projects from this medial angle over the medial part of the eyeball. In the rhesus monkey this is a much more prominent structure than in man. It is a membranous fold and is not supported by cartilage as in some of the other mammals.

OCULAR MUSCLES

(Figs. 102, 116, 117)

There are eight muscles within the orbit, the levator palpebrae superioris to the upper eyelid, and two oblique, four recti and one accessory lateral rectus to the eyeball.

The *levator palpebrae superioris* muscle has its origin from the upper margin of the optic foramen. It lies just above the superior rectus muscle. It passes forward and becomes fan-shaped as it inserts into the substance of the upper eyelid, chiefly into the tarsus.

The *recti* muscles are named according to their position as *superior*, *lateral*, *inferior* and *medial*. All four of these have their origin from a ring of fibrous connective tissue (annulus tendineus communis) which bounds the optic foramen. They extend from the optic foramen to the eyeball a little anterior to its equator, and insert by means of tendinous fibers respectively into the superior, lateral, inferior and medial aspects of the eyeball.

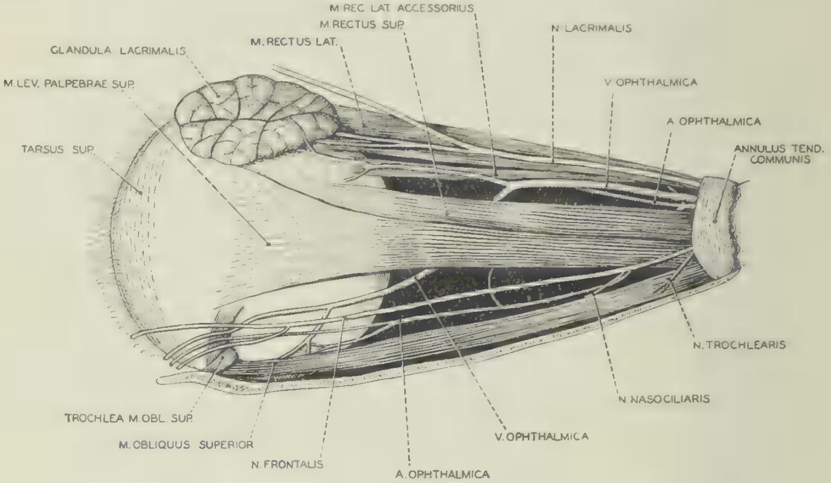

FIG. 116. Right eye from above, showing muscles, nerves and blood vessels.

The *oblique* muscles are the superior oblique and the inferior oblique. The *superior oblique* has its origin at the margin of the optic foramen between the superior and medial recti. It is a slender muscle which passes forward along the medial part of the orbit to the anterior margin of the cavity, where it forms a narrow tendon which passes through a special fibrous pulley or trochlea attached to the superomedial margin of the orbit. As the tendon of the muscle passes through the pulley it makes a short bend and passes laterally to the insertion of the superior rectus and inserts on the eyeball partly under cover of the latter (fig. 116). The *inferior oblique* muscle has its origin from the medial part of the floor of the orbit just behind its anterior margin. It swings laterally over the insertion of the inferior rectus, bends around the eyeball and inserts into it partly under cover of the external rectus muscle (fig. 117).

The *accessory lateral rectus* muscle (also termed m. retractor bulbi, rectus posterior, choanoides) lies beneath the lateral rectus. It is a distinct muscle throughout its length. It arises just beneath that of the lateral rectus and inserts on the eyeball between the lateral and superior recti, but more posterior than the recti. It is innervated by a branch of the *abducens* nerve. In most of the author's dissections this is a prominent muscle about $\frac{1}{4}$ to $\frac{1}{3}$ the size of the lateral rectus, but in a few cases it is a thin fibrous band in which scattered muscle fibers are distinctly discernible This muscle occurs in man only as a rare variation.

NERVES OF THE ORBIT

(Figs. 102, 116, 117)

The nerves which are found in the orbit are infra-orbital (n. maxillaris), n. lacrimalis, n. frontalis, n. nasociliaris, n. oculomotorius, n. trochlearis, n. abducens and n. opticus. Of these the n. maxillaris, n. lacrimalis, n. frontalis and n. trochlearis lie in the peripheral part of the orbital fossa while the others lie deeper.

The *n. maxillaris* or infra-orbital nerve is a branch of the trigeminal nerve and lies, as the name indicates, below the eye in the infra-orbital groove in the floor of the orbit and is covered by the peri-orbital fascia.

The *n. lacrimalis* lies in the supralateral part of the orbit in the orbital fascia above the ocular muscle. It sends branches to the lacrimal gland and to the fascia and skin on the lateral side of the orbit. It is also a branch of the trigeminal nerve.

The *n. frontalis*, another branch of the trigeminal nerve, lies in the supramedial part of the orbit above the ocular muscles. It passes along the upper medial side of the orbit to the region of the trochlea where it divides into the n. supra-orbitalis and n. supratrochlearis.

The *n. nasociliaris*, a branch of the trigeminal nerve, enters the orbit just medial to the origin of the external rectus muscle. In the orbit it divides into a number of branches. The first branch is the so-called *long root of the ciliary ganglion.* It passes above the ciliary ganglion, is met by a nerve from the latter which fuses with it and then passes forward to enter the posterior part of the eyeball (fig. 117). The course of this branch is not always the same, for in a few of the author's dissections it passed through the edge of the ciliary ganglion. As the nasociliary nerve swings medially beneath the superior rectus muscle it gives off several small nerves (*nn. ciliares longi*) to the posterior part of the eyeball. The nerve then courses medially and forward where it gives off the *n. infratrochlearis* and then penetrates the medial wall of the orbit and enters the mucosa of the nose.

The *n. oculomotorius* enters the orbit through the sphenoidal fissure and immediately divides into a superior and an inferior branch. The superior supplies the superior rectus and the levator palpebrae superioris muscles. The inferior branch passes forwards, and after giving branches to the medial and inferior recti ends in the inferior oblique muscle. Just above the root of the inferior branch of the oculomotor nerve is the *ciliary ganglion* lying on the lateral side of the optic nerve. It is connected to the inferior branch by a very short thick nerve. From the ganglion a variable number (usually 4 or 5) *short ciliary nerves* pass forward to the posterior part of the eyeball, which they enter.

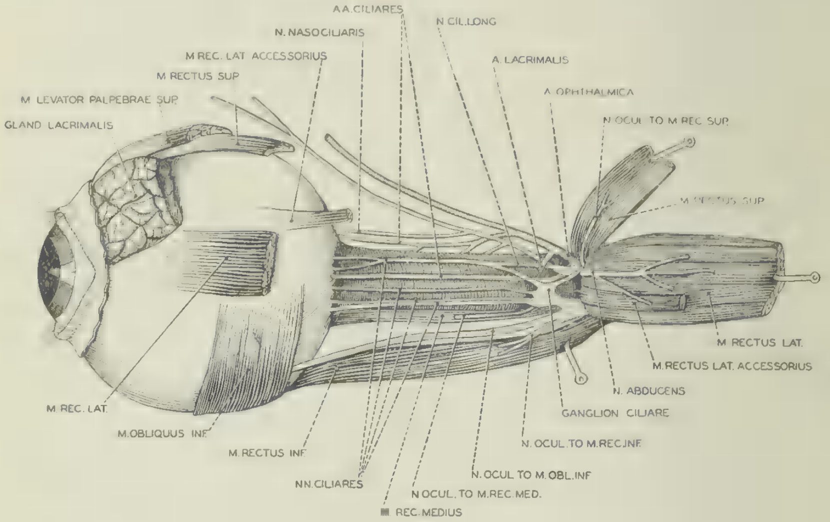

FIG. 117. Left eye, lateral aspect, showing muscles, nerves and blood vessels.

The *n. trochlearis* enters the orbit through the sphenoidal fissure above the eye muscles and supplies the superior oblique muscle from above.

The *n. abducens* enters the orbital fossa through the sphenoidal fissure just below the oculomotor nerve and supplies the lateral rectus and the accessory lateral rectus muscles.

The *n. opticus* is a thick, cord-like nerve which enters the orbital fossa through the optic foramen and passes forward to enter the posterior pole of the eyeball. It supplies the retina.

BLOOD VESSELS IN THE ORBIT

Arteries (figs. 116, 117). The blood supply to the orbit is through the *ophthalmic artery*. Before entering the orbit it gives off the *central retinal artery* which passes to the eye through the optic nerve. As the ophthalmic artery enters the orbit beneath and between the superior and lateral recti muscles it sends off a number of branches: (1) the *lacrimal artery*, which is prominent, and which passes forward under cover of the corresponding vein between the superior and lateral recti muscles to the lacrimal gland, lateral part of the eyelid muscles and possibly gives rise to some of the anterior ciliary arteries; (2) *muscular branches*, two of which are quite large, one to the lateral and accessory lateral recti and one to the superior rectus and levator palpebrae superioris; (3) *posterior ciliary arteries*, which are three or more in number and vary in different eyes. In one of the author's preparations (fig. 117) there were several small and one large posterior ciliary artery. The latter passed forward between the optic nerve and ciliary ganglion and with the short ciliary nerves to the eyeball. After these branches are given off the ophthalmic artery swings medially between the optic nerve and the superior rectus muscle and then forward in the space between the levator and superior oblique. It then breaks up into a number of small branches, the muscular, supra-orbital, ethmoidal, palpebral, nasal and frontal.

Veins (see fig. 116). There are usually two ophthalmic veins in the orbit, the *v. ophthalmica inferior* and the *v. ophthalmica superior*. The former is small, draining the structures in the inferior part of the orbit. The superior ophthalmic vein is prominent, as shown in figure 116. It lies above the ophthalmic artery. Halfway between the posterior part of the orbit and the eyeball it divides into two main branches, one to the lateral part of the orbit and lacrimal gland and the other passing medially beneath the superior rectus to the medial part of the orbit. These veins drain the parts supplied by the ophthalmic artery. The veins draining the eyeball are known as the *venae vorticosae* and are four or five in number. They leave the eye a little posterior to the insertion of the eye muscles. One of these venae vorticosae is shown in figure 116 leaving the eyeball and joining the lacrimal vein.

THE EYEBALL (BULBUS OCULI)

The eyeball is situated in the anterior part of the orbital fossa in part surrounded by the ocular fascia. On it are attached the extrinsic ocular muscles.

The eyeball is not quite spherical, being composed of the segments of two spheres, viz. an anterior smaller transparent, corneal segment and a posterior, larger, opaque, scleral segment. The anterior segment, because of its shorter radius, projects as a dome in front of the scleral part. The anterior segment and part of the sclera surrounding it lie in the conjunctival sac and are covered by the ocular conjunctivum, whereas the rest of the eyeball is surrounded by the ocular fascia.

The eyeball consists of a wall of three coats, the outer or *sclera*, the middle or *choroid* and the inner or *retina*. Inside the wall is the eye cavity, within which is a biconvex transparent lens located in a meridional plane between the anterior and posterior segments. This lens divides the eye cavity into two compartments, the anterior and posterior. The *posterior compartment* is filled with the transparent *vitreous humor* and the *anterior compartment* with *aqueous humor*. The anterior compartment is further subdivided into an anterior and a posterior chamber by the diaphragm or *iris*, which is the anterior projection of the choroid coat.

Coats of the eye

There are three coats of the eye.

1. THE OUTER COAT of the eye is the *sclera* and *cornea*. The sclera covers the posterior three-quarters of the eyeball and the cornea the anterior remaining part of the eye. The sclera is a dense connective tissue which serves as a protective coat to the eye and also as a medium for the attachment of the accessory eye structures. The anterior part of the sclera, which lies in the conjunctival sac, is thicker than the rest of the sclera and forms a white band around the cornea. It is lined by the ocular conjunctivum. On the inner surface of the sclera is a thin layer of pigmented connective tissue, the *lamina fusca*. Near the posterior pole of the eyeball, where the optic nerve enters, the scleral coat is perforated by the fibers of the optic nerve and by the retinal artery. This part of the sclera is known as the *lamina cribrosa sclerae*.

The *cornea* forms the wall of the anterior part of the eye. It is a thick, firm, transparent connective tissue coat lined on the outside by the ocular conjunctivum and on the inside bordering the anterior chamber by the thin inner corneal epithelium. The margin of the cornea is intimately fused with and continuous with the white part of the sclera.

2. THE MIDDLE COAT of the eye is the *choroid*. It is a highly vascular, pigmented connective tissue layer which lies on the inner surface of the sclera. At the outer limit of the sclera it bends into the anterior com-

partment to form the diaphragm or *iris*, which divides this space into the anterior and posterior chambers. Behind the iris at the plane of the lens the choroid is considerably thickened and is thrown into a large number of meridional folds, the *plicae ciliares*. This modification of the choroid forms a ring-like body, the *ciliary body*. Within this body are numerous smooth muscles, the *ciliary muscles*, which are for the most part arranged in a meridional plane, although some are circular. The *intrinsic muscles* are smooth muscles and are all located within the choroid coat. Besides the *ciliary muscles* there are *iridial muscles*. Two sets of these are described: (1) the *circular*, which lies in the iris around the pupil, and which is prominent in the rhesus monkey; (2) the *meridional fibers*, which are not noticeable even in histological section, and whose presence in the rhesus monkey is questionable.

3. THE INNER COAT of the eye is the *retina*. It is divided into two parts, the visual and the non-visual retina. The *visual retina*, which is sensitive to light, consists of an outer layer of pigmented epithelium which lines the choroid coat and an inner layer of neuro-epithelium and modified terminal portion of the optic nerve. It lines the posterior compartment of the eye as far forward as the posterior margin of the ciliary body, where the neuro-epithelium and nerve fibers end. This region is called the *ora serrata*. The *non-visual* retina, which is primarily pigmented epithelium, continues over the ciliary body and posterior surface of the iris and becomes continuous with the epithelium which lines the anterior chamber.

THE LENS is a biconvex transparent body situated beyond the iris. It is more convex posteriorly than anteriorly. The lens is surrounded by a thin, strong, transparent membrane, the *lens capsule*. This capsule is attached along the equator of the lens by fine transparent fibrous bands, the *suspensory ligaments of the lens*, to the ciliary body. This area of fibrous bands between the lens and ciliary body is known as the *zonula ciliaris* or zonule of Zinn.

THE EAR

The ear of the rhesus monkey is similar to that of man and consists of three chief divisions, the external, middle and inner ear.

EXTERNAL EAR

The external ear is subdivided into a lateral or external expanded portion, the auricle (auricula), and a canal, the external auditory meatus, extending from the auricle to the middle ear, from which it is separated by the tympanic membrane.

Auricle. The auricle is composed of an internal framework of elastic cartilage to which are attached numerous small muscles and which is covered by integument. The shape of the auricle therefore is determined by the shape of the cartilage, except for the lobule, which has no cartilaginous support. The auricles are attached to the sides of the head. From the point of attachment around the opening of the external auditory meatus each auricle expands in the superior, posterior and inferior directions. Each auricle is somewhat pyriform in shape. The irregular concave lateral surface is tilted slightly forward. The auricle thus resembles a very irregular, anteriorly incomplete funnel, whose apex surrounds the opening of the external meatus. The rim of the auricle is thickened, due to the rolling up of the cartilaginous framework in a lateral direction. In some monkeys this folding is absent along the posterior margin. This rim, which describes an irregular arc, is the helix. At the antero-inferior end of the helix is the lobule, a cartilage-free expansion of the integument. It is not as prominent a structure as the lobule in man. At the superior, slightly posterior margin the helix has a pointed, somewhat thickened, bent over projection which resembles an inverted cone. This is Darwin's tubercle. Within the helix, but separated from it by the scaphoid fossa, is a ridge, the antihelix, which lies parallel to the posterior part of the helix. The antihelix is branched superiorly into a crus anterior and a crus superior. Within the antihelix is a deep conical concavity, the concha,which leads to the external auditory meatus. This concavity is overlapped from in front by a tongue like flap, the tragus, and from below just above the lobule by the antitragus. The notch between these two flaps is the incisura intertragica.

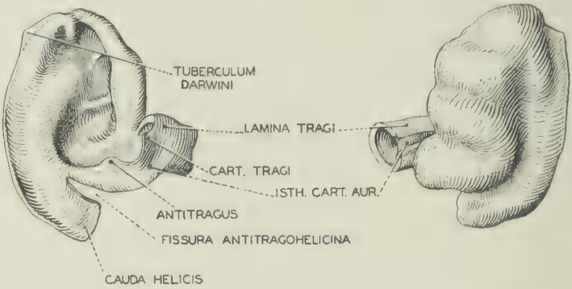

Fig. 118. Lateral and medial views of the cartilages of the right auricle.

In general the auricle of the rhesus monkey has more irregular curves and ridges than that of man and is less massive.

THE CARTILAGE OF THE AURICLE (fig. 118). The cartilage, while it gives shape to the auricle, is not present in all parts. Between the inferior crus of the antihelix and the cauda helicis there is a break in the cartilage called the fissura antitragohelicina. The inferior crus of the antihelix terminalis is the antitragus. Anterior to the antitragus the cartilage of the concha is narrowed to form the isthmus cartilaginus auriculae and then expands to form the lamina tragi. This lamina differs from that in man in that it bends on itself to form an almost complete ring around the external opening of the external auditory meatus. The free edges of the incomplete ring are held together by dense connective tissue fibers. At its medial margin this ring fits over the outer rim of the cartilage of the external auditory meatus and is united to it by dense connective tissue fibers, which permits movement between the two cartilages. The most external part of the external auditory meatus must therefore be considered as being made up and supported by the lamina tragi.

MUSCLES OF THE EXTERNAL EAR. (See chapter VIII.)

EXTERNAL AUDITORY MEATUS (fig. 119). The external auditory meatus consists of three parts, the outer, middle and inner. The outer is supported by the ring-like lamina tragi of the auricle. The middle part is short and is supported by the cartilage ring of the meatus. The inner half of the meatus is a bony canal. The entire external auditory meatus is lined by stratified squamous epithelium from which many ducts lead to the ceruminous glands imbedded in the underlying connective tissue cerumen.

THE MIDDLE EAR OR TYMPANIC CAVITY

(Figs 119, 105)

The tympanic cavity (cavum tympani) is an irregular, somewhat flattened, elliptical-shaped air chamber in the bulla of the temporal bone. It lies between the inner end of the external auditory meatus (from which it is separated by the tympanic membrane) and the anterior surface of the bony periotic capsule. The cavity is divided into two portions, the lower or tympanum proper and the upper or recessus epitympanicus. There is no definite separation between these two portions except that the cavity is constricted between them, and the stapes and tendon of the tensor tympani muscle cross at this plane.

The tympanum proper is quite large, comprising almost two-thirds of the cavity and the epitympanic recess only about one-third. In man the latter is larger than the former. The tympanum contains three small ossicles, the incus, stapes and malleus. The tympanum proper contains the manubrium of the malleus and its medial wall is perforated by the opening of the eustachian tube. The epitympanic recess contains the head of the malleus and the incus and the mastoid antrum communicates with it through its posterolateral wall. The mastoid antrum is a wide opening and can hardly be considered as an antrum since the smoother wall of the epitympanic recess goes over gradually to the broken wall of the mastoid air cells without any noticeable constriction between the recess and the mastoid air spaces.

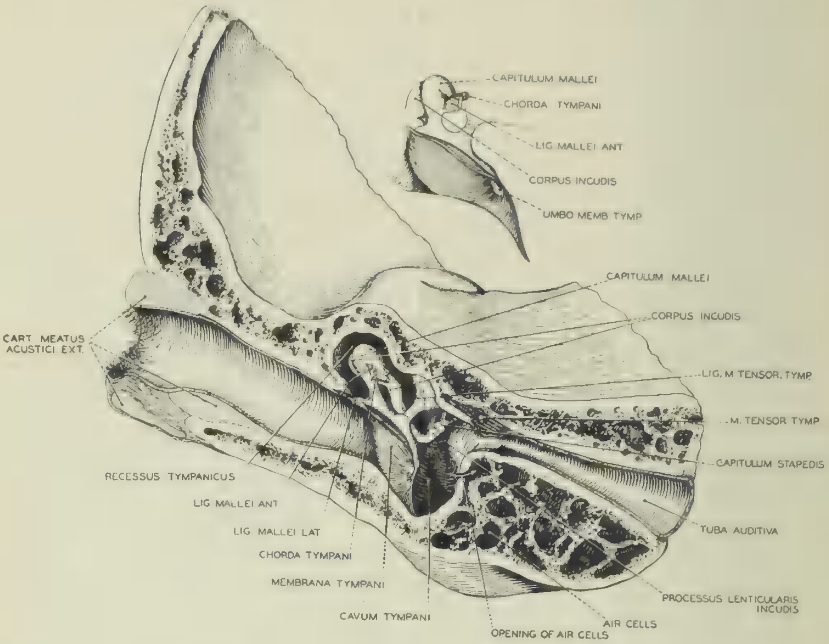

Fig. 119. Section of temporal bone to show external auditory meatus, middle ear structures and eustachian tube.

The petrous bone forming the medial wall of the tympanum proper, through which the eustachian tube passes, is also very porous and contains, as far as can be determined, many air cells (fig. 119). Histological sections through this region show small communications between the tympanum and these air cells.

The tympanic cavity is lined by a mucous membrane which is continuous through the eustachian tube with that of the nasopharynx. This mucous membrane is supported by the bony wall of the tympanic cavity except over the tympanic membrane and over the fenestra rotunda (fenestra cochleæ), where bone is absent. Above the fenestra rotunda the foot plate of the stapes fits into the oval depression (fenestra vestibuli) in the posterior wall of the tympanic cavity. The bony plate of the stapes here fills the gap produced by the oval-shaped absence of periotic bone. The mucous membrane here is reflected over the stapes and covers the chain of ossicles as well as the tendons and ligaments attached to these bones. These ligaments will be described with the ossicles.

The nerve-supply of the middle ear is through the tympanic plexus. The chorda tympani nerve passes through the tympanic cavity but does not contribute to its innervation.

The tympanic membrane

The tympanic membrane is a thin elliptical semitransparent fibrous membrane which forms a partition between the external auditory meatus and the middle ear. Its circumference is attached to a groove (sulcus tympanicus) at the inner end of the bony external auditory meatus. It is stretched across the inner end of the external auditory canal at an oblique angle, so that the inferior part of the membrane is much further removed from the outside than the superior part. On the middle ear side the manubrium of the malleus is attached to the membrane a little inferior to its center. The tensed malleus exerts a pull on the membrane at the point of attachment, so that the membrane is slightly cone-shaped, with the apex of the cone or umbo directed towards the tympanic cavity. The membrane is lined on the middle ear side by the mucosa of the tympanum and on the outer surface by the integument of the external auditory meatus.

Ossicles of the middle ear

There are three small bones in the middle ear, the malleus, incus and stapes (figs. 119, 120).

THE MALLEUS. The malleus consists of a long slender arm, the manubrium, whose free end is attached to the umbo of the tympanic membrane. The other end is constricted to form the neck, which connects with the thickened, rounded part, the head, which articulates with the incus. On the lateral surface of the malleus, where the neck and manubrium join, is the lateral process, to which is attached the lateral ligament of the malleus. This fastens the malleus to the upper, inner end of the bony external auditory meatus at the notch of Rivinus (fig. 119). On the anteromedial aspect of the head of the malleus is a bony process, the anterior process of the malleus (figs. 119 and 120), to which is attached the anterior ligament of the malleus. This anterior process of the malleus is the ossified remnant of Meckel's cartilage. On the posteromedial side of the manubrium there is a small protuberance to which is attached the tendon of the tensor tympani muscle.

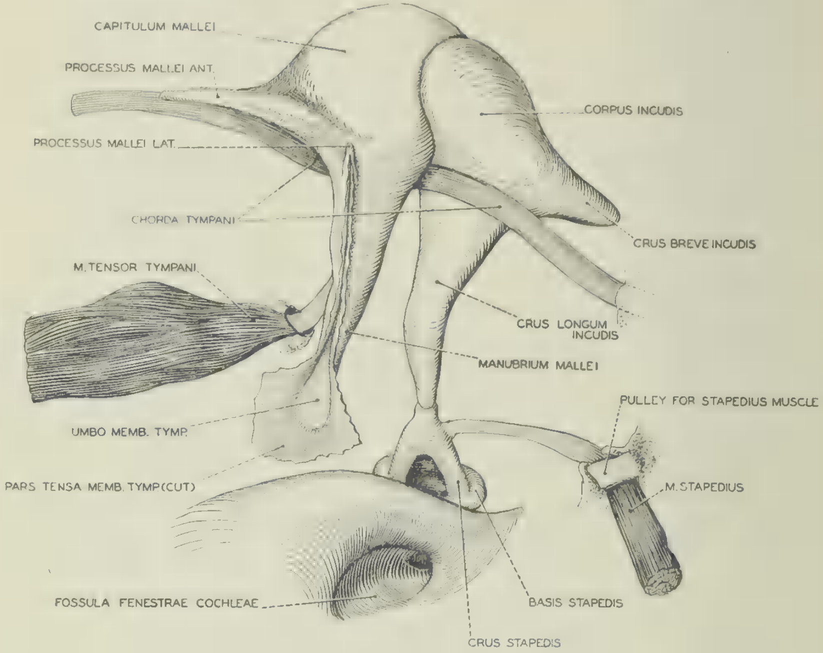

FIG. 120. The auditory ossicles.

THE INCUS. The incus consists of a body with a short posterior process and a long ventromedial process. The body has a concave surface which articulates with the head of the malleus. The short arm extends posteriorly and is fastened to the wall of the tympanic cavity by the posterior ligament of the incus. The free end of the long arm articulates with the head of the stapes.

THE STAPES. The stapes is shaped like a stirrup. It consists of a head which articulates with the incus, a foot plate or base which fits into the fenestra vestibuli of the petrous bone, and two crura, the medial and lateral, which connect the base with the head. The base is held in place by the annular stapes ligament, which unites the base to the petrous bone forming the margin of the fenestra vestibuli. The tendon of the tensor tympani muscle is attached to the lateral crus of the stapes near its junction with the head of the stapes.

Muscles of the middle ear

M. TENSOR TYMPANI. This has its origin from and lies within a bony canal just above the eustachian tube. This bony canal extends along the posterior wall of the tympanum above the promontory. Above and a little medial to the stapes the muscle leaves the canal, bends at a right angle and by means of its tendon stretches across the narrow part of the tympanum to insert on the manubrium of the malleus. At the place where it leaves the bony canal there is a dense connective tissue pad attached by fibrous bands to the bony wall to form a pulley or sling over which the tendon acts.

M. STAPEDIUS (figs. 119 and 120). This has its origin from and lies in a bony canal similar to that of the m. tensor tympani, just medial and parallel to the facial canal, where it lies below the level of the stapes. Contrary to most descriptions this is a rather long muscle within its canal. At the level of the stapes it leaves the bony canal through an aperture in the pyramidal eminence, bends at a right angle and by means of its tendon inserts on the lateral crus of the stapes near its junction with the head of the bone. At the place where the muscle leaves the bony canal there is a dense connective tissue pad, attached by fibrous bands to the bone, which serves as a pulley over which the muscle acts (fig. 120).

THE INTERNAL EAR

The internal ear or labyrinth is enclosed by the bony otic capsule of the petrous portion of the temporal bone.

Openings in the otic capsule

In the dry otic capsule five perforations can be seen.

1. THE FENESTRA VESTIBULI. Into this opening the foot plate of the stapes fits.

2. THE FENESTRA COCHLEARIS. During life this opening is spanned by a thin membrane known as the secondary tympanic membrane. It separates the scala tympani of the cochlea from the middle ear.

3. THE INTERNAL AUDITORY MEATUS. It admits the cochlear, vestibular, and facial nerves.

4. THE CANAL FOR THE AQUAEDUCTUS COCHLEAE. It is a canal filled with loose periotic tissue and perilymph. It is a communication between the scala tympani and the arachnoid spaces of the meninges in the region of the internal auditory meatus.

5. THE CANAL FOR THE AQUAEDUCTUS VESTIBULI. This is a membranous canal which is a communication between the otic or endolymphatic labyrinth and the endolymphatic sac which lies in the dura in the region of the lateral sinus.

The labyrinth

The labyrinth is composed of the soft tissue, which, with its fluid filled cavities, fills the cavity of the otic capsule. This labyrinth can be divided into two parts, the *periotic labyrinth* (also known as the perilymphatic portion of the internal ear) and the *otic labyrinth* (also termed the endolymphatic portion). The former lines the cavity of the otic capsule and surrounds the otic or endolymphatic labyrinth. The periotic labyrinth therefore contains the otic labyrinth within itself.

THE PERIOTIC LABYRINTH (fig. 121). The periotic labyrinth consists of an expanded part, the *vestibule*, which is continuous laterally into *three semicircular canals*. These are the superior, posterior and lateral. At the upper end of the lateral and superior canals, where they join the vestibule, each has an enlargement due to the enlarged endolymph canals, called the ampulla. These ampullae open together into the upper part of the vestibule. The posterior semicircular canal has its ampulla at its lower end where it opens into the lower part of the vestibule. The other ends of the canals open into the lateral side of the vestibule. The superior and posterior fuse into a common canal, the crus commune, which opens into the upper lateral part of the vestibule. The lateral canal opens into the vestibule just below the crus commune and immediately above the ampulla of the posterior canal.

Inferomedially the vestibule continues as a tubular structure coiled like a snail shell. This is the *cochlea*. The bony otic capsule which covers the apex of the cochlea bulges into the middle ear and forms the promontory. The core of this snail shell like cochlea is a part of the bony otic capsule and is known as the modiolus. A spiral shelf of bone from this modiolus, the lamina spiralis, incompletely divides the periotic tissue of the cochlea lengthwise into two parts, the scalae. At the apex of the cochlea this spiral shelf is incomplete and is here known as the

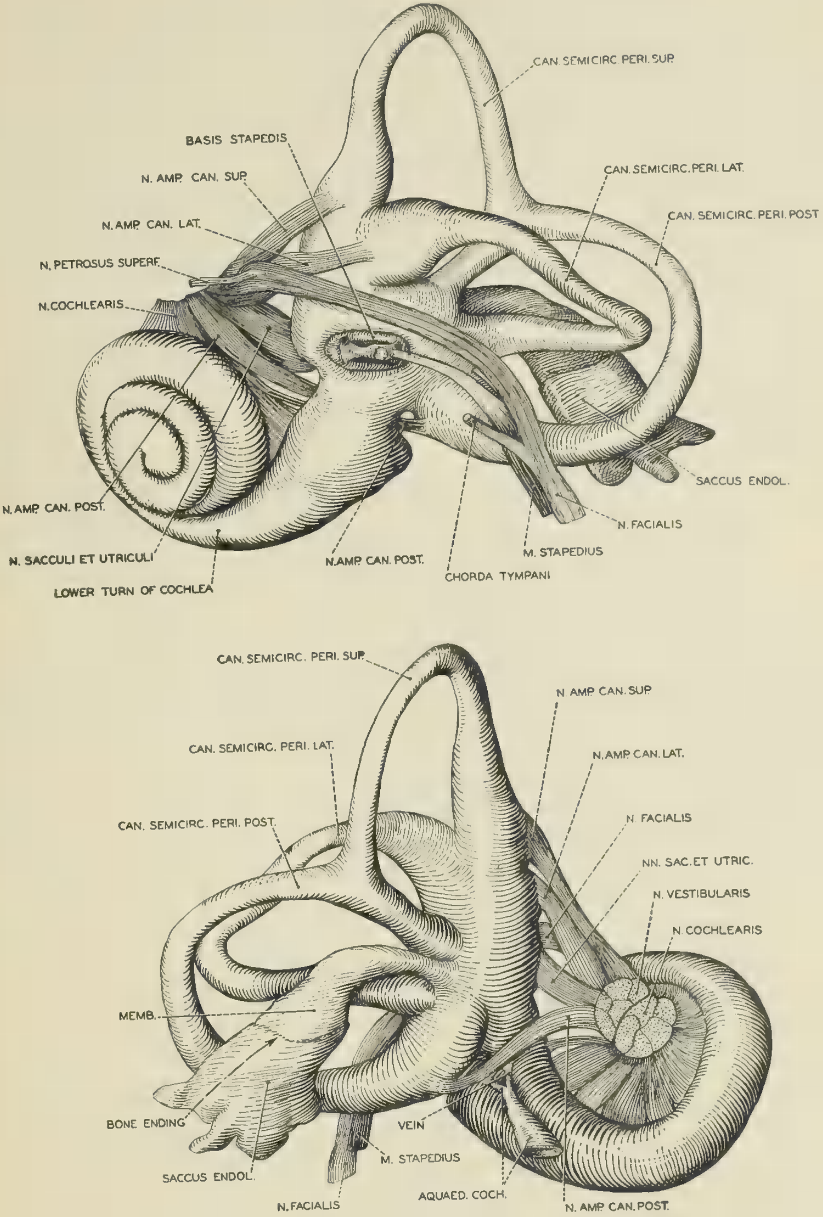

FIG. 121. Anterior and posterior views of periotic labyrinth.

hamulus. At this point the two scalae communicate with each other by an opening, the helicotrema. A dense lamina of connective tissue stretched between the free end of the bony spiral lamina and the bony otic capsule completely separates the two scalae except at the helicotrema. The two scalae are known as the *scala tympani* and *scala vestibuli*.

The scala tympani begins at the fenestra cochlearis, where it is separated from the middle ear by the secondary tympanic membrane, and constitutes the anterior part of the cochlear tube. At the apex of the cochlea it communicates through the helicotrema with the scala vestibuli, which forms the posterior part of the cochlear tube and communicates with the inferomedial part of the vestibule.

The periotic labyrinth is made up of connective tissue which forms a dense layer along the bony otic capsule, but which is of a very loose character within the labyrinth and contains large spaces and channels occupied by the periotic or perilymphatic fluid. In the vestibule these spaces are so extensive that they can be regarded as forming a sac containing the periotic fluid. Only scattered connective tissue fibers stretch across this sac along the periphery. In the cochlea the scalae are completely hollowed out and form ducts containing the periotic fluid.

The periotic spaces, which are continuous throughout all divisions of the periotic labyrinth, can be considered as a closed system except for the aquaeductus cochleae, which connects the scala tympani with the arachnoid spaces of the meninges.

THE OTIC LABYRINTH OR ENDOLYMPHATIC SYSTEM (fig. 122). The otic labyrinth is a system of tubes and sacs lined by epithelium contained within the periotic labyrinth. This system consists of three semicircular canals and their ampullae, the utriculus, the sacculus, the ductus cochlearis, the ductus saccularis, the ductus utricularis, the ductus endolymphaticus, and the saccus endolymphaticus.

The *ductus cochlearis* lies within the cochlea between the scala tympani and the scala vestibuli. It is separated from the scala tympani by Reissner's membrane and from the scala vestibuli by the lamina spiralis ossea and the basilar membrane. It starts blindly at the apex of the cochlea and ends blindly as the cul-de-sac within the vestibule. Near this cul-de-sac the cochlear duct communicates with the base of the sacculus by means of a fine duct, the *ductus reuniens*. Within the cochlear duct is the *organ of Corti*, which extends throughout its length except at its vestibular end.

The *sacculus* lies in the medial portion of the vestibule. It has an

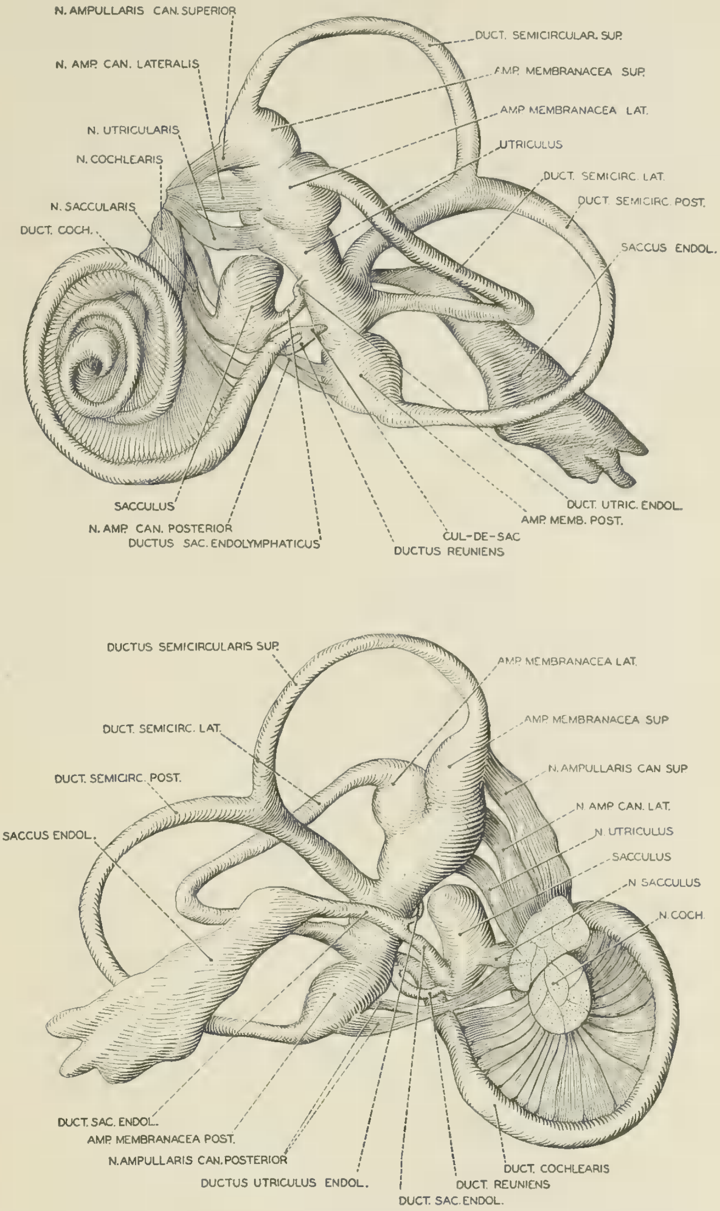

Fig. 122. Anterior (above) and posterior (below) views of the otic labyrinth.

irregular oval shape. Near its base just posterior and above the entrance of the ductus reuniens a duct, the *ductus saccularis*, leaves the saccule. This duct is joined by the small *ductus utricularis* to form the *ductus endolymphaticus*. The latter passes posteriorly, emerges from the vestibule, passes through the bony otic capsule and ends in the *saccus endolymphaticus*, which lies within the dura mater in the region of the lateral sinus.

The *utriculus* is a thick tubulosaccular structure and lies within the vestibule. On its medial side it is connected with the ductus endolymphaticus by the ductus utricularis. Above it is joined by the ampullar ends of the superior and lateral semicircular canals, below by the ampullar end of the posterior semicircular canal, posterolaterally by the crus commune, or common duct of the superior and posterior semicircular canals, and inferolaterally by the lateral semicircular canal. All three canals lie eccentrically within the connective tissue of the periotic canals.

NERVES OF THE OTIC LABYRINTH. The VIIIth cranial nerve supplies the internal ear. It is divided into two parts, the cochlear nerve and the vestibular nerve. The cochlear nerve supplies the organ of Corti. The vestibular nerve sends separate branches to each of the ampullae of the semicircular canals, to the macula of the sacculus, and to the macula of the utriculus.

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APPENDIX

HOUSING AND CARE

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HOUSING

The new quarters of the Carnegie Monkey Colony at Baltimore and those of the Rochester University School of Medicine, Rochester, N. Y., embody certain desirable features which are the outcome of some years of experience in the care of monkeys on the part of Dr. George W. Corner and as well as of the present writer. These quarters will be described with the aid of simplified plans and sketches to show how the prime needs of air, light and exercise as well as of temperature and humidity control have been met. These points involve general principles applicable both to new quarters designed and built specifically for housing monkeys and to old space adapted to the purpose. In any event, protection against the weather (rain, cold, summer's sun) and access to the open air all contribute to the success of the undertaking.

THE CARNEGIE MONKEY HOUSE

The new Carnegie Monkey House (Messrs. Archer and Allen, Architects, Baltimore) comprises an additional story (the 6th) atop a laboratory building of the Johns Hopkins University School of Medicine. As seen from the accompanying sketches (figs. I, II and III), it consists of a series of paddocks ranged along the north and the south sides of a row of three laboratories or work rooms. The middle room, provided with a skylight, is used as kitchen and examining room and is directly accessible to the vestibule leading to the paddock. These are of somewhat different sizes to accommodate various numbers and combinations of animals; for since rhesus monkeys are inveterate fighters and display strong personal likes and dislikes towards one another, it is important that only mutually agreeable groups be confined in the same paddock. Mature males must be housed singly.

The *floors* of the paddocks are of tile, those of the laboratories of mastic, in order to facilitate quick and thorough cleaning. The floors are routinely swept and then washed with hot running water. There is one drain to every two paddocks, with one large overflow drain in each corner of the building to take care of excess rain water.

The *roof* over the laboratories, it may be noted, has a broad overhang which protects not only the vestibule, but also, for a space of 16 inches, the paddocks as well, thus affording the monkeys shelter against either rain or sun.

For *perches*, broad boards have been found to be inappropriate, since they cup in the weather and therefore hold rain water and feces and are difficult to clean. Moreover, such shelves greatly increase the difficulty of catching the animals with the net. Instead of boards, 2 x 3's set on edge seem ideal. They are bolted to the cage at convenient intervals (fig. III). To enable the animals to lean comfortably while resting, the perches stand out about two inches from the side of the cage. These narrow perches are practically self-cleaning and furthermore offer no impediment to catching the animals with a

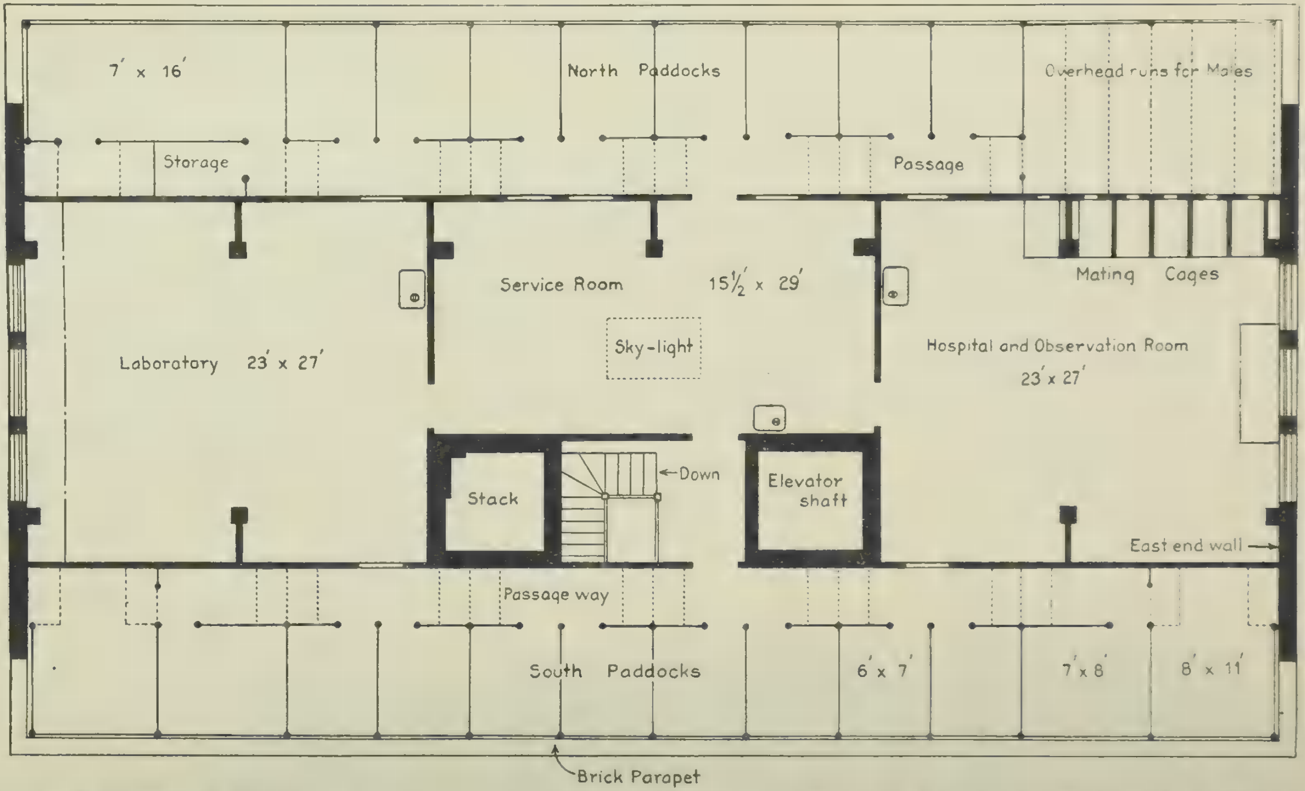

FIG. I. Floor plan of the Carnegie monkey house erected on top of a laboratory building at the Johns Hopkins Medical School. Hutches are shown by dotted lines. (This and the next two figures are taken from the 1932 report of the Carnegie Institution of Washington; sketches by J. F. Didusch.)

net. Similar perches are placed inside the hutches, since some animals sleep sitting up, at least part of the time.

The *hutches* should, if possible, be placed outside the paddocks. If this is done, the paddock will be free of all encumbrance by eliminating all awkward corners where the animals might crouch and avoid capture. In the Carnegie Colony the hutches are placed overhead in the vestibule or passage (see illustrations), where they are protected against the weather and are likewise well out of the way. A hutch communicates with the paddock to which it belongs by means of a single hole about 7 x 9 inches. A trap door operated from the vestibule by a lever enables one to lock the animals in or out of the hutch. Since it is important that this trap door remain either open or closed, as desired, it is fastened into place with snap-hooks. In winter weighted canvas flaps further protect the occupants of the north-side hutches against direct drafts.

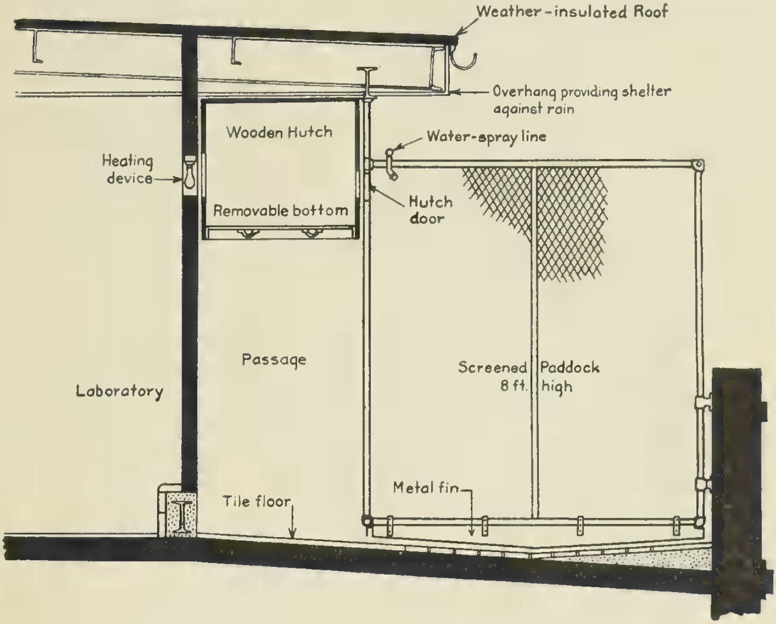

FIG. II. Section through a typical paddock (see text).

The inside of the hutches is accessible to the attendants both by double side doors and by the removable metal bottoms. The latter are removed for the weekly cleaning, the former are used to replace the layer of mill shavings and of hay which constitute the bedding. The hay has to be replaced oftener since most of it may soon be eaten by the monkeys. The side doors are, furthermore, necessary to drive the animals out into the paddock to effect their capture when desired.

The *wire tops and sides* of the paddocks admit the sun's rays the year round, though on the north side only a portion of the paddock is exposed to the direct rays. In the hottest months, however, it may be necessary on the south side to reduce the amount of sunlight by means of boards laid over the tops and wired down. The writer wishes to express a warning against the use of brass bolts in such iron work, as they do not stand the stress. Many had to be replaced by heavily galvanized steel bolts.

To *temper the excessive heat* of the Baltimore summer still further it has been found desirable to use an overhead sprinkler system. This is permanently installed, though of course drained in winter. Each paddock has an outlet with nozzle that throws a fine mist-like spray into one side of the paddock, leaving the other side dry. The occupants give every evidence of appreciating the cooling spray, since they alternately go under it to gather beads of water on their hair and allow it to evaporate in the breeze. We feel that this cooling system is, in this climate, more essential than the heating units in winter.

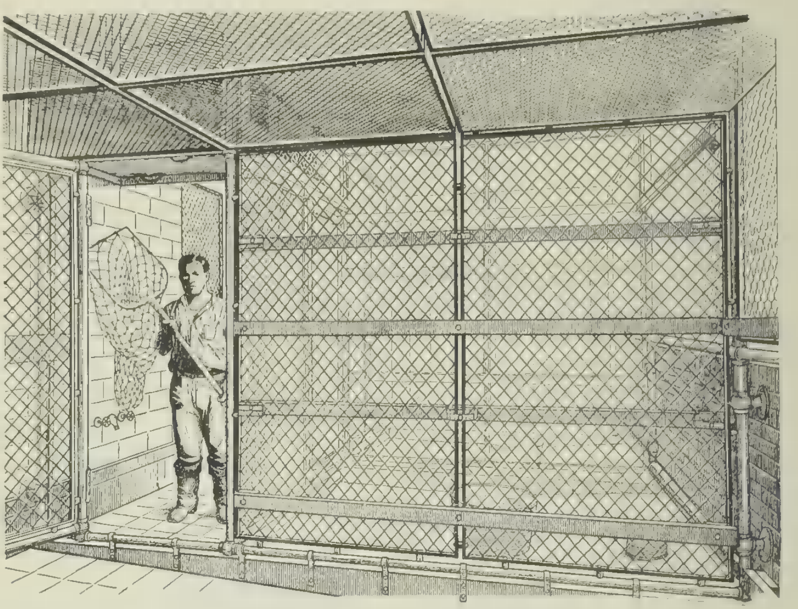

Fig. III. Sketch showing general character of paddocks and vestibule. Note arrangement of perches.

The *heating units* consist of two ordinary 100-watt electric light globes in receptacles set into the tile wall, a unit for each hutch. The lights are protected against the occupants of the hutch by means of a perforated iron plate. In the severest weather, when both globes are turned on, the hutches are quite comfortable, i.e. about 50° or 60° F.

Water is provided in ordinary galvanized washtubs. Occasionally mischievous groups will learn to splash out the water, upset the tubs and bang them about, in which case it is necessary to chain the tubs to the paddock wall. In hot weather the spray keeps the tubs filled.

The *food dishes* are cast of iron after a pattern designed by O. O. Heard of our laboratory. Due to the shape as well as the weight (8½ pounds) the monkeys are unable to upset the dishes or to damage them.

In addition to the paddocks it is necessary to have isolation or "hospital" cages, which are placed in a room that can be kept warm. We make these cages very simply and in units, so that the cages may be used singly or ranged side by side in a row. The frame is made of straight, clear 2 x 3's. The ledges where feces might otherwise catch are beveled off.

These units are six feet tall and 30 inches deep and mostly 30 inches wide. The back and top are of stout, ½-inch meshed wire cloth stapled permanently to the frame. There is no bottom; but a cage or a row of them, instead of standing directly on the floor, may be set on a platform covered with ¾-inch meshed wire cloth, of No. 12 wire, somewhat elevated from the floor. The cage may be made into a "double-decker" by means of a partition or slide consisting of similar heavy wire cloth mounted on ⅜-inch iron frame. This may be slid on tracks consisting of L-irons screwed to the frame. For this purpose a 3-inch space may be left between the upper and lower doors.

The sides of each cage consist of wire cloth stapled to separate frames made of 1 x 3-inch strips. Such a frame is "demountable." Thus, when it is desired to make a double-sized cage out of two cages, opposite sides are removed and the cages fastened together side by side.

The doors, an upper and a lower to each cage, are best made of channel iron frames and woven wire. (No. 11 wire, 1½-inch diamond shaped meshes, ¾-inch channel iron.) The door has two features of convenience: First, it contains a small set-in service door 9 x 9 inches at the lower margin. Through this door the animal may be serviced without danger of its escaping. The second feature is the drinking cup removable from the outside. The cup is placed into a hole left in the large door and has a flange that prevents the animal's pulling it into the cage; a metal strap suitably fastened in place with a snap-hook on the outside prevents its falling out.

The iron work has been intelligently done for us by F. H. Plack, Enterprise Wire and Iron Works, Baltimore.

THE UNIVERSITY OF ROCHESTER MONKEY HOUSE

We are indebted to Dr. George W. Corner for the following notes and floor plan descriptive of the Monkey House at the University of Rochester School of Medicine and Dentistry:

"This was designed for long-term study of *Macaca mulatta* under fairly severe climatic conditions (extremes of official temperature about −7°F. (−22°C.) and +100°F. (+38°C.) Messrs. Gordon and Kaelber, Architects, of Rochester, N. Y., drew the plans from the author's sketches.

"This structure (fig. IV) was erected on the roof of a larger building previously built, and its design and construction were partly determined by that fact. The plan shows an inner room (its unnecessarily large size and irregular shape were determined by the existing building below) and a series of shelters (A and B, fig. IV). Two of these shelters at the northeast corner are 7 x 8 feet and communicate with outside runs 8 x 13 feet. These will accommodate up to twenty-five animals each. Two shelters (at the southwest corner) intended for individual males, are 4½ x 6 feet and communicate with runs of the same size. The remaining ten are 3 x 6 feet with runs of the same size. These are larger than is absolutely necessary for single animals, but were made large enough to permit free movement of a man with a net in his hands. The relatively large size gives plenty of room for exercise and also permits housing two or three animals when necessary.

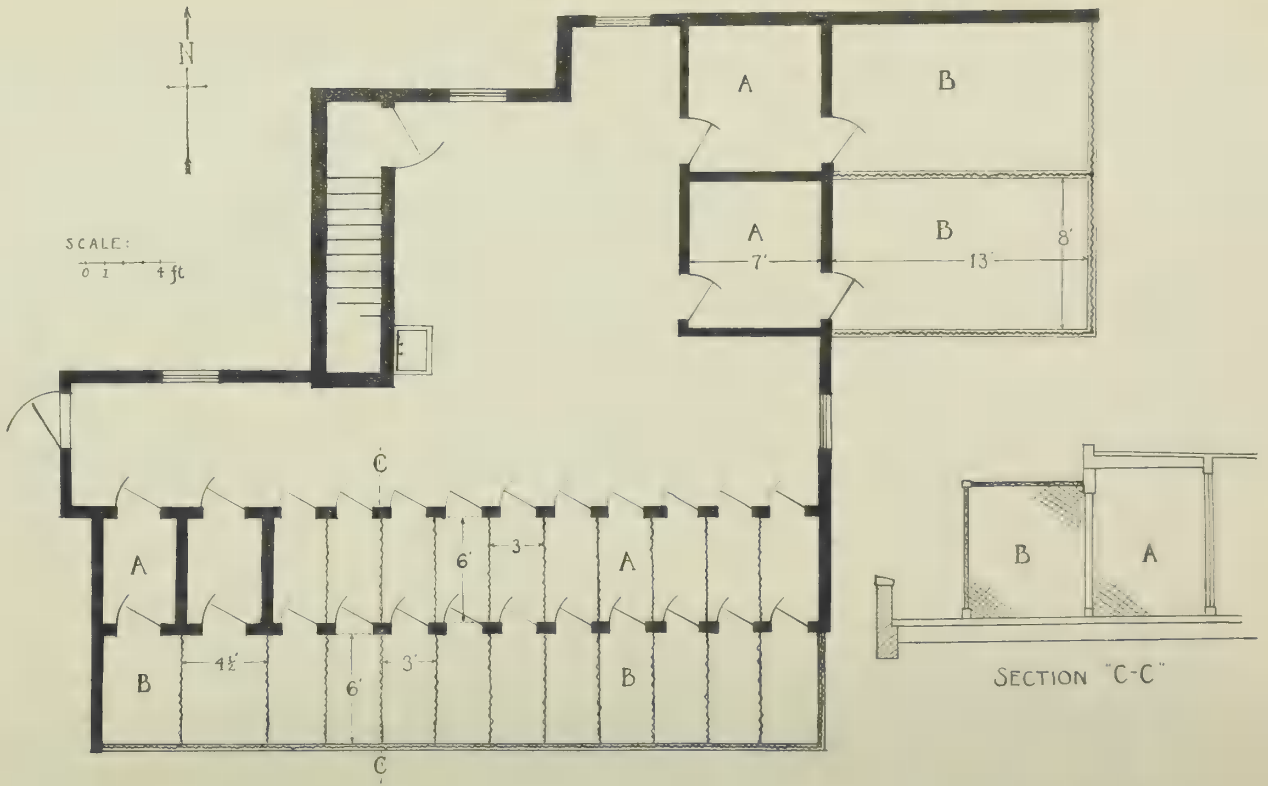

Fig. IV. Floor plan, with section through a typical paddock, of the monkey quarters built atop a laboratory building at the Rochester University School of Medicine and Dentistry. (Sketch by Dr. George W. Corner.)

"The shelters are about 7 feet 9 inches high inside, the runs 7 feet. Each shelter is equipped with a removable wooden shelf high on the wall, for the animals to sit on.

"The outer wall of the building is extended along the north and west to shelter the runs from north and west winds.

"For the sake of lightness the walls are made of two layers of wood with cinders between; tile or brick would be better. The floor of the whole structure, including the runs, is of mastic, and is pitched gently toward suitably placed floor-drains.

"The walls and ceilings of the runs and the partitions between the shelters are of diamond mesh No. 10–1½ galvanized wire link fabric. All doors and other wood surfaces exposed to the monkeys are covered with galvanized sheet iron. All doors exposed to the monkeys are equipped with thumb-locks on the outside.

"The inner room is heated in winter, and the doors between this room and the shelters are hung about ½ inch above the sills in order to allow a little warmth to enter the shelters. A special type of latch has been designed to allow the doors to stand slightly ajar in very cold weather. At night in winter and also by day in the coldest weather the doors between the shelters and the runs are closed and the animals are thus kept practically indoors but not at full room-temperature.

"The arrangement here described permits free access in the open air in all but the coldest weather, with shelter from the sun in summer and from snow and wind in winter."

CATCHING THE ANIMALS

Before discussing methods of catching monkeys a word of warning will not be amiss: There should always be more than one door between the monkeys and the freedom of the outer world. This safeguard may be brought about by means of a vestibule placed before the paddock entrance. The common vestibule or passage shown in figures I to III serves the same purpose. Latches should be constructed so that they may be fastened with snap-hooks or locked with a padlock.

Breeding cages should have movable partitions for separating male and female, for it is best not to attempt to handle the larger males.

In the Carnegie Colony the animals are all caught by means of a net (figs. III and V). The net is thrown over the animal, which is then brought to the floor of the paddock. If the net consists of ample folds, the captive is easily shaken down until it stands or lies on the paddock floor. It is best first to grasp the animal by the back, say across the iliac crests, after which first one, then the other elbow is brought over the back so that with one hand both elbows may be grasped and the animal thus placed under absolute control. Most rhesus monkeys may be safely carried in this way, with one hand, leaving the other free for opening doors and the like; but some of the larger females and all the big males usually require the use of both hands.

As the net now in use in the Carnegie Colony is a development and embodies features found by trial and error to be efficient, a detailed description will prove of value. The iron frame is of the shape shown in figure V (12 x 16 inches). The top margin is straight so as to prevent the monkey's dodging out from under the corners. The bottom may be rounded as shown, which, of course, gives the greatest space in proportion to weight. The iron is fastened into grooves cut on either side of a hickory handle. To effect attachment the iron is brought down into two straight shanks, which in turn end in short hooks embedded into shallow holes in the handle. It should be noted that these shanks are of different lengths so that the holes in the handle may be staggered and undue weakening of the handle thus avoided. The iron frame is then wired to the handle. Three-eighths inch wrought iron seems to be the ideal size for the frame, which should stand heavy daily use for a number of years.

The nets are made as separate units entirely independent of the frames, because the wear and tear on the net falls upon the parts that strike the cage walls. Hence the net is first woven and then lashed to the frame with cords, which, when they wear out, are readily replaced.

The opening of the net is of the circumference of the frame, of course; the net should be about three feet deep. The tendency is to make the net too shallow. The meshes are two inches to the side (4 inches "stretched"); our nets therefore measure 20 meshes around the rim and 11 meshes deep. We have found No. 2 cotton rope to be of a convenient weight and strength. Our nets are woven by the R. J. Ederer Net and Twine Co., 16 E. Lombard Street, Baltimore.

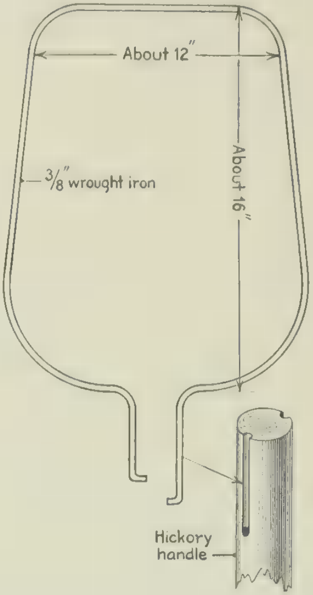

FIG. V. Sketch of frame of net used in catching monkeys in the Carnegie Colony.

Such is the method used daily in the Carnegie Colony for routine examination of the animals. The animals soon become accustomed to being caught and for the most part surrender as soon as caught. Hence it is believed that the experience is rather beneficial than the opposite for them.

For some situations the trapping method, such, for example, as that employed by Dr. Edgar Allen, may be found convenient. It is through Dr. Allen's cooperation that we are enabled to sketch his set-up.

The monkey quarters consist of an inside cage or retreat and an outside paddock; these communicate through door *A* (fig. VI). The former is divided into two compartments

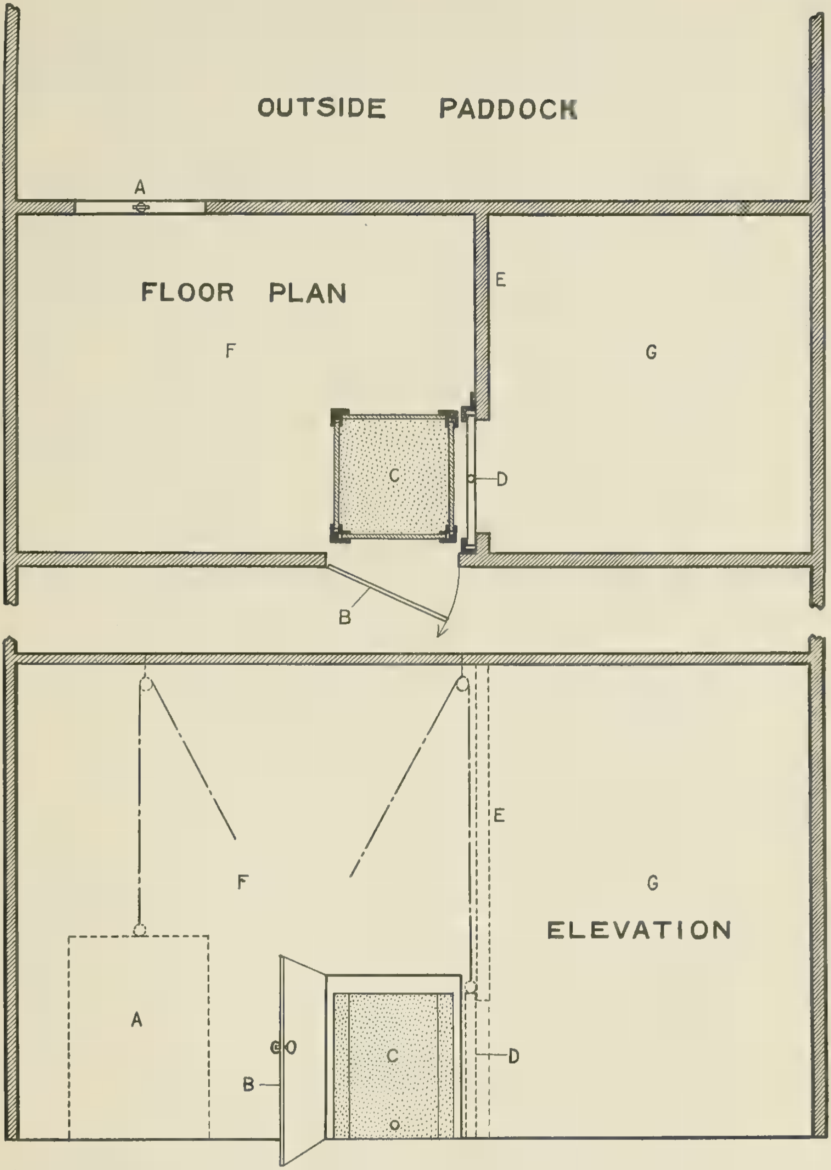

Fig. VI. Floor plan and elevation of paddock used by Dr. Edgar Allen at the University of Missouri Medical School. (Sketch by J. F. Didusch.)

(*F* and *G*) which are separated by a partition (*E*) provided with a drop door *D*. The swinging door *B* in the back of the cage allows the attendant to place a trap cage *C*, large enough to hold two monkeys, before trap door *D*. When both doors of the trap cage as well as trap door *D* are open at the same time, the animals may pass freely between the compartments, which they learn to do readily. By closing the appropriate trap doors upon the animals as they enter the trap cage they may be imprisoned in the trap cage, which is then removed through door *B*.

To handle the animals, they are caught by the attendant, who protects his hands with leather gloves. However, if it is necessary to inject the animals frequently, use is made of a three-inch hole cut in one corner of the cage. Through this the animal soon learns to present first one leg and then the other for injection.

This method has perhaps the advantage of exciting the animals less than by running them around the paddock with a net, though the excitement of the restraint and the struggle for freedom is still too great to secure norms of temperature or pulse. For such purposes it is necessary to have thoroughly trained and gentle animals. It is hoped that persons who have such records secured on trained animals will let the editor have the benefit of them.

FOOD

The most important single item in the care of monkeys is that of food. It is even possible to keep a monkey indoors in a good state of health on a proper diet. Thus, Mr. Otto Heinzer, caretaker in the Department of Pathology, Harvard Medical School, has kept four rhesus monkeys in good health for a period of eight years in an indoor laboratory cage 5 x 4 x 3 feet. The diet used was very much like that used in the Carnegie Colony with the exception of eggs.

Dr. George W. Corner has had long experience with monkeys and now furnishes his colony the following diet:

The chief ingredient is the proprietary food, "Purina Dog Chow," large checkers (Ralston Purina Co., St. Louis). An adult female eats about 15 bricquettes ("checkers") daily. A second meal consisting of fresh food is given daily, as follows: Raw eggs, two to each animal, once weekly; bananas or orange, carrots, lettuce, tomatoes (canned or fresh according to the season) are fed in moderate amounts, varying the fruit or vegetables from day to day.

The diet of the Carnegie Colony is a little more varied, though perhaps no better. Dog Chow is the staple diet on Sundays, along with peanuts or sunflower seed and a vegetable or sprouted oats—a single feeding that has to last for the day. Two feedings are made on all week-days. Powdered milk ("Parlac" or "Klim") is fed on bread or boiled rice almost every day; eggs twice a week, each animal receiving three to four. Many kinds of vegetables and fruits are fed, according to season and price. A typical weekly schedule is as follows:

	Morning	*Afternoon*
Monday	Milk and rice	Sweet potatoes and sprouts
Tuesday	Bread, milk, eggs	Bananas, white potatoes, grains
Wednesday	Milk and rice	Cabbage, carrots, sweet potatoes
Thursday	Milk and rice	White potatoes, lettuce, grains
Friday	Bread, milk, eggs	Sweet potatoes, radishes, carrots
Saturday	Milk and rice	Beets, spinach, grains
Sunday	Dog Chow, peanuts, sun-flower seed, onions	

Onions, both raw and boiled, are relished. The potatoes are sometimes boiled, but more often fed raw. The grains are corn, wheat and rolled oats. Wheat germ is sometimes sprinkled over the milk and rice. Sprouted oats are sometimes fed on Sunday. Meat has never been given; but there is a question in our minds whether insects as well as viscera of animals would not be a good thing for the monkeys. Milk has been found to be toxic to a few animals, causing diarrhea, which stops in these cases when the amount of milk is reduced and a grain diet temporarily substituted. Mr. Heinzer has stopped diarrhea in his monkeys with boiled milk, partly skimmed. Reduction in amount of "greens," increase in proportion of grains or dog chow is helpful. It is easy to overdo the feeding of greens. Caretakers should watch the consistency of the animals' feces, which should be firm enough to stand up in a pasty lump where it drops on the floor.

Of this treatment Dr. Corner says: "Rhesus monkeys do well under this regime. Tuberculosis and acute primary pneumonia are unknown, and the chief illness seen is a sudden anorexia and asthenia of unknown cause, usually followed by death in two or three days, with no autopsy findings except interstitial pneumonia. The only infectious disease observed has been Flexner dysentery, of which we had one severe epidemic. The senior animal of the present colony, a male about 14 years old, has remained in perfect health during 6 years residence in this building and 4 previous years in a simple outdoor run with only a thin wood box for shelter."

The same may be said of the Carnegie Colony. But two cases of lobar pneumonia have occurred here. The few cases of tuberculosis that were found were infected when they arrived. One advanced case of the disease recovered, as careful autopsy later showed (#48, see Hartman, Contributions to Embryology, 1932, p. 135).

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